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FISHING WITH THE OTTER

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The otter is an amphibious "beastie," whose general shape of body, whose webbed feet and whose power of remaining under water fit him admirably for an aquatic life. Add to these factors an extraordinary rapidity in swimming (greater than that of most fishes) and an insatiable appetite for fish food, and one can see that one of the otter's chief businesses in life is the chasing, capturing and devouring of fishes. Consequently it is not strange that among various peoples in various parts of the world, the otter has been domesticated and his piscatory inclinations and activities turned to the profit of his master.

A—Otter-Fishing in Asia

Otter-fishing originated and has longest been carried on in Asia. In fact, it is the only continent in which such a method of taking fishes is in vogue to-day. It seems at the present to be carried on in three Asiatic countries—China, Malaya and India.

I—In China

The people who seem first to have tamed the otter and to have used it in catching fishes are the Chinese. One of the first and best known European travelers in China [1275–1292] was Marco Polo, but we look in vain in his

pages for any reference to otter-fishing. Likewise in Friar Odoric of Pordenone (in China, 1323–1328), we look in vain for otter-fishing in the *ordinary* versions; however, one extraordinary version tells another story. But there is yet another old traveler, Sir John Mandeville, of blessed memory, and to him we must go for our earliest printed account of fishing with the otter.

The earliest dated copy (1480) of the marvelous adventures of our much traveled old knight bears title, "Ce Livre Est Appele Mandeville et Fut Fait et Compose par Monseir Jehan de Mandeville Chevalier Natif Dangleterre de la Ville Sainct Alein," etc. There are also Italian and Latin editions of 1480, and there are undated editions which may possibly have been printed earlier. The earliest English version seems to be that of Pynson—"The Boke of John Maunduyle Knight"—undated but published sometime between 1493 and 1498. This was republished by John Ashton in 1887 in somewhat modernized spelling, but otherwise without change. Here is his account of otter-fishing:

> In this countrey [in the Kingdom of Mancy or Manzi, that part of China south of the Hoang-ho River] they take a beast that is called Loyres, and they keepe it to goe in to waters or ryvers, and straighte waye hee bringeth out of the water great fishes, and thus they take fishe as longe as they will, and as them nedeth.

In the magnificent folio edition of "The Buke of John Maundevill," an unpublished English version found in the Egerton MS. 1982 in the British Museum, with George F. Warner[1] as editor, we read in the old English that "in this land thai take a beste that es called Loyres, and thai teche him to ga in to waters and riuers, and alssone he bringes oute grete fischez, als many and as oft as thai will."

In 1725 there was published in London an English version from the text in the Cotton MS. (Titus C xvi). This I have not seen, but in 1839 a reprint[2] was issued at

[1] Printed for the Roxburghe Club, Westminster, 1889, p. 102.

[2] "The Voiage and Travail of Sir John Mandevile Kt." J. O. Halliwell, editor, London, 1839, p. 209. This text is from the Cotton MS. *circa* 1400. A verbatim reprint of this at London, 1866.

London under the editorship of J. O. Halliwell. Here is our quotation from this version:

Also in that Contree, ther ben Bestes, taughte of men to gon in to Watres, in to Ryveres and in to depe Stankes [tanks] for to take Fysche: the whiche Best is but lytille and men clepen hem Loyres. And whan men casten hem in to Watre, anon thei bringen up great Fissches, als manye as men wold, and zif men wil have mo, thei cast hem in azen, and thei bryngen up als many as men list to have.

Here the word *loyres* or *loirs* means otter. Littré writes it *loutre* from the Latin *lutra*. The medieval Latin word *lutra* or *luther* is found in the Gouda (*c.* 1484) and Coloniae (*c.* 1500) editions in the New York Public Library and in the works (presently to be referred to) of Vincent de Beauvais (1480) in the New York Public Library and of Albertus Magnus (1495) in the Library of the American Museum. In the Provençal dialect the word was written *leure* or *lorre, loiria* or *luria.* The Italian versions have it *udria* (Venice, 1491, in the New York Public Library), *utria* or *idria* (Bologna, 1870). The Sanskrit word is *udra.* But everywhere and always it is the otter, the "water dog."

In the days when the early versions and editions of Sir John were issued it was believed that he was a veritable person, who was born and bred in England at the town of St. Albans, traveled between 1322 and 1357 over practically all the whole known world, wrote his book of adventures in French and published it in MS. form between 1357 and 1371, and that he died and was buried in Liége, Belgium, in 1372. But modern research reveals no contemporary English records of such a John de Mandeville. On the other hand, the evidence seems to point to the writing of the "Voiage and Travailes" by a Liége physician named "Jean de Bourgoyne dit à la Barbe." The whole matter is shrouded in mystery and is only of passing interest here. For a discussion of the matter (certainly one of the most complicated and extraordinary in all literature) see Mandeville in the Encyclopædia Britannica, 11th ed., vol. XVII.

Whoever the compiler may have been, it is certain that the "Marvellouse Adventures" of joyful memory are a

compilation and that that part dealing with the kingdom of Mancy is "lifted" from the travels of Friar Odoric of Pordenone. Odoric was in China about 1323–1328. He dictated his travels to an amanuensis in 1330 and during the following year died. His book was first printed (in Latin) at Pesaro in 1513, but before that it had existed in MS. form, the great numbers of which MSS. attest its widespread popularity. In Odoric the fishing in the province of Mancy is with cormorants, as I have shown in another paper.[3] Here the account reads as follows from the earliest English version:[4]

> And . . . I traueilled 18. dayes iourney further, and came vnto a certain great riuer, and entered also into a city whereunto belongeth a mighty bridge to passe the said riuer. And mine hoste with whom I soiourned, being desirous to shew me some sport, said vnto me: Sir, if you will see any fish taken, goe with me. Then hee led me vnto the foresaid bridge, carying in his armes with him certaine diue-doppers or water-foules, bound vnto a company of poles, and about euery one of their necks he tied a threed, least they should eat the fish as they tooke them: and he carried 3. great baskets with him also: then loosed he the diue-doppers from the poles, which presently went into the water, & within lesse then the space of one houre caught as many fish as filled the 3. baskets: which being full, mine host vntyed the threeds from about their neckes, and entering the second time into the riuer they fed themselves with fish, and being satisfied they returned and suffered themselues to be bound vnto the said poles as they were before.

Now if Mandeville copied "Frier" Odoric, and if Odoric wrote of Cormorant-fishing in the province of Mancy, how did Mandeville convert cormorants into otters? Is this a true account or did Mandeville make the change that his book might not too closely resemble Odoric's? This question has for a long time puzzled critics and editors, but I believe that the explanation is not far to seek, and as I see it here are the facts, which

[3] Gudger, E. W., "Fishing with the Cormorant: I—In China." AMERICAN NATURALIST, 1926, Vol. 60, pp. 5–41. 16 Figs.

[4] Hakluyt, Richard, "The principall Navigations, Voyages, Traffiqves and Discoueries of the English Nation, Made by Sea and Ouer-land to the South and South-east Parts of the World at any Time within the Compass of these 1600 Yeres." London, 1599, folio. Also in the London reprint, 1810, and in the Maclehose reprint of the "Principal Navigations." Glasgow, 1904, Vol. IV, p. 425.

were dug up in the course of a careful investigation of all the early cormorant-fishing stories.

The first edition of Odoric was in Latin at Pesaro, 1513; the second in French, Paris, 1529. Next come two Italian versions in Ramusio's "Navigationi et Viaggi," Veneto, 1583. In one of these versions the cormorant-fishing story is started but is left incomplete, the other contains this amazing variation:[5]

> Mine host . . . took us to one side of the bridge where the river was wider, and then we found many boats, and there was one of them employed in fishing by aid of a certain fish called *Marigione*. The host had another such, and this he took and kept it by a cord attached to a fine collar. And this indeed is a creature that we have seen in our own seas, where many call it a *sea-calf*. It had the muzzle and neck like a fox's, and the forepaws like a dog's, but the toes longer, and the hind feet like a duck's [*i.e.*, webbed], and the tail with the rest of the body like a fish's. Mine host made him go in the water, and he began to catch quantities of fish with his mouth, always depositing them in the boat, and I swear that in less than two hours he had filled more than 2 big baskets.

This plainly refers to the otter and is so accepted by all hands. My explanation for this apparent discrepancy is that Odoric saw in the south of China *both* the cormorant and the otter used for fishing, that he narrated both accounts, that the majority of MSS. got the cormorant as the agent but that others had the otter as the chief factor in the account, and finally that Ramusio incorporated into his book one of these latter manuscripts. *Marigione,* a variant of *maragone,* simply means diver, and the otter is even more a diver than the cormorant—spending much more of his life in and under water than does the bird. Cordier's French edition of Odoric has the word *plungons.*

I have examined nineteen editions of Mandeville, ranging in date from 1484 to 1919—eleven English versions; one Gaelic; one Swedish; one Danish; two Latin (1484? and 1500?); and three Italian (1491, 1497, 1870)—and all

[5] Yule, Sir Henry, "Odoric of Pordenone," Vol. II of "Cathay and the Way Thither, being a Collection of Medieval Notices of China," translated and edited by Col. Sir Henry Yule. New edition revised . . . by Henri Cordier. London, 1913, Hakluyt Society, 2. series, Vol. XXXIII, pp. 188–191.

use the word otter or its appropriate translation. These versions have their origins in at least a half dozen manuscripts. There is every reason to believe that every MS. and every printed edition and version of Mandeville's travels has the account of otter-fishing and never that of the use of cormorants. My explanation is that Mandeville for his original MS. and Ramusio for the 1583 edition of his "Navigationi et Viaggi," both used the same version or MS. of Odoric—*i.e.*, that one containing the account of *otter-fishing.*

But the question may be raised as to what proof there is that fishing with the otter was carried on in China and specifically in the south of China where Odoric undoubtedly saw the cormorant used. The answer is that (as will be abundantly shown later) fishing with the otter is carried on in the Yangtze region of China to-day, and, in a country where customs are so firmly fixed and come down from long time past, it seems *a priori* very probable that otter-fishing was practised not only in Odoric's time but long before. However, let *a priori* reasoning be ever so strong, it is not proof, and the inquirer has a right to demand proof.

At this point, unable to find any references to the old Chinese literature which would help, I wrote to the distinguished Chinese scholar, Dr. Berthold Laufer, curator of ethnology in the Field Museum, Chicago. Dr. Laufer had previously given me some data on early Chinese accounts of cormorant-fishing antedating Friar Odoric. Here again he was able, from his wide knowledge of Chinese ethnological matters, to make me his debtor. I have pleasure in quoting his notes *verbatim:*

Chang Tsu, a writer of the Tang dynasty (608–916), in his work *Chao ye tsien tsai,* states that within the boundaries of Tung-chwan [the old name for Ta, which forms the prefectural city of Sui-ting fu in Se-chwan] there are many otters living by the river side, each reared by its own master. The tail-feathers of a pheasant when placed in front of its den keep the otter inside; when the feathers are removed, the otter leaves its den and ascends the river bank in order to fish. The men capture a large portion of the fishes and then allow the otters to satisfy their appetite. They drive them back into their dens by striking a stick on the ground, and close them up again with the pheasant's tail-feathers.

The *Yu yang tsa tsu,* written about A. D. 860 by Twan Cheng-shi, contains this notice, "At the end of the period Yüan-ho (A. D. 807–821), there lived in the district Yün-hiang (now Yün) in Kün chou (Hu pei) a man seventy years old who raised ten otters for the purpose of catching fish."

Sung Ki (998–1061), in his book *Pi ki,* quotes a certain Wang Tse-huan as saying that he saw with his own eyes at Yung chou (in Hu-nan) tame otters kept for fishing in the place of cormorants; they daily caught about ten catties of fish, enough to supply the want of a family; some of the otters were able to pierce a turtle.

Li Shi-chen, author of the *Pen tsao kang mu* (end of 16th century), writes that in Se-chwan and Mien (a district in Han-chung fu, Shen-si), tame otters are commonly kept for the purpose of fishing and that they are very skilful.

Referring to this same Li Shi-chen, the orientalist, Stanislas Julien, sent to J. F. Brandt a communication entitled, "Notice sur le Castor (Loutre et Enhydris)." Brandt wrote an extensive series of papers on these animals, and included the "Notice" in an article, "Mittheilungen über den Biber, wohl richtiger die Fisch- und Meerotter, aus chinesichen Schriftstellern nach Stanislas Julien" in *Memoires Academie Imperiale Sciences,* Saint Petersburg, 1855, 6th series, vol. 7 (Nat. Sci.), pp. 359–360. Li-chi-tchin (as his name is written by Julien) composed his great work (as cited by Dr. Laufer) in the period of Wan-li (1573–1620). Julien's French translation of his title is "Grand Traite d'Histoire Naturelle sans Rapports avec la Medicine," and in this Li says "Nowadays the fishermen train tamed otters (*Loutres*) to catch and bring home fishes, a thing of which they acquit themselves with surprising agility."

Here then we have confirmation of Mandeville's and the Ramusio-Odoric accounts of otter-fishing in China in Chinese works covering a period of from say 700 A. D. to 1600 A. D. It should be noted specifically that Li's book was published in China about one hundred years after the appearance in print of the earliest edition of Mandeville.

Here then we have the proof that otter-fishing in China goes back into the remote past, certainly to a date prior to 600 or 700 A. D.—how much earlier can not certainly be said. Now it should be noted that this fishing in all the citations given by Dr. Laufer was practised in the

Yangtze basin, and I shall now show that to-day otter-fishing is practised in the same region of the erstwhile Celestial Empire. It is significant, however, that there is a jump in these accounts from about 1600 to 1870, a gap of 270 years.

In a previous paper I have brought together a large number of early accounts of cormorant-fishing in China. A rather careful search through the same early travels in China which brought such interesting accounts of the use of the cormorant reveals no word of otter-fishing. However, the explanation is not far to seek. The early travelers in China (especially those quoted on cormorant-fishing) rarely saw any parts of the Celestial Empire save the coastal cities and the regions round about, or at most they hardly penetrated farther than the Grand Canal. Cormorant-fishing is and was especially practised on the streams crossing the great plain of China, while, as the data now to be presented will show, otter-fishing seems to be confined largely to the upper and mountainous parts of the Yangtze and its tributaries. This is probably due to the fact that the otter in all likelihood is not found in the thickly populated open plains country where there is little chance of its finding hiding places, but is rather a dweller in the upper rocky stretches of these streams where shelter abounds and hiding places are frequent.

Probably a minute search of the literature would bring to light accounts of fishing with the otter in China to fill in the space between Li (about 1600) and Swinhoe (1870) now to be quoted, but this has not been done because in the absence of any references whatever the labor would far exceed the income. Swinhoe[6] in 1870 gives the following interesting account:

> In the Ichang Gorge, 1,110 miles up the river Yangtsze, we came across a fisherman with a trained Otter. It was very tame and gentle, but he kept it chained in his boat. To make use of its services he would throw his large loose net, weighted at the edges, and let the Otter into the water

[6] Swinhoe, Robert, "Catalogue of the Mammals of China (South of the River Yangtze) and of the Island of Formosa." Proceedings Zoological Society London, 1870, p. 625.

fastened by a long string: the Otter would swim and dive round the outer edge of the net, driving the fish under the net, which gradually contracted its edges until it was drawn up. The fisherman would then call the Otter, giving him a jerk or two, and it quietly returned to its corner in the boat.

Swinhoe makes it clear that the otter does not catch the fishes but merely drives them into the net. So also Maurice Jametel alleges in his book, "La Chine Inconnue," Paris, 1886 (3rd ed.), p. 208, when he says: "The . . . [otter], which one finds often on the upper courses of the river Bleu, is trained by the fishermen to drive fishes into the nets which they cast, and it acquits itself of this function with as much ease as do the better trained of our hunting dogs." It has not been possible to locate this river Bleu.

During the early seventies of the last century Armand David traveled throughout China and made extensive natural history observations. The library of the American Museum has an English separate, purporting to be a translation from the "Nouvelliste," entitled, "Natural History of North China," by Père Armand David. On page 36 one reads: "During the voyage across Kiangsi, Hoopeh and Szechuen [in the Yangtze drainage], Father David observed with admiration otters quite as tame as cormorants. At the command of the fisherman, these animals throw themselves into the water and bring back the fish to the master's bark." Here the otter catches the fishes and brings them one by one to its master. I have searched through all David's works to be found in New York, but as all lack indices I have not been able to locate the original references.

Miss Gordon Cumming ("Wanderings in China," new ed., London, 1887, p. 103) tells us that the Chinese on the upper Yangtze in the neighborhood of Tchang (Ichang?) have learned to convert this keen fish poacher into an efficient game keeper and helper. She specifically notes that nowhere else in China did she hear of such a use.

In this same upper region of the Yangtze (near Ichang) Percival[7] (1889) found the fishermen using huge dip nets.

[7] Percival, Wm. Spencer, "The Land of the Dragon: My Boating and Shooting Excursions to the Gorges of the Upper Yangtze," London, 1889, pp. 128–129.

He gives some details either peculiar to this region or overlooked by others. To make these nets more effective a trained otter wearing a muzzle is put overboard. "The otter runs about the bottom, swims around, and drives all the fish he can into the net. After a lapse of time the net is hoisted and the otter comes up with it." These beasts are very tame, they come when called and are handled and cared for by their masters with perfect safety. A well-trained one commands a high price. Notable is the point that the otter comes up *inside* the net.

The well-known zoological collector, A. E. Pratt, in the first part of his interesting book, "To the Snows of Thibet through China" (London, 1892, p. 24), describes his ascent of the Yangtze and tells us that at Ichang, "Situated on the opposite bank of the river . . . is a small village, known to Europeans as the 'Otter Village,' from the fact that the natives there make use of otters for fishing. These otters may be seen every day tied up in the bows of the sampans, and appear to be quite tame."

Hosie[8] (1897) found otter-fishing practised at Hsing-lung-ch'ang on the Ching-lin, a tributary of the T'o, which is itself a tributary of the Yangtze between Chung-king and Chau-fu. This account establishes a record much farther west and higher in the mountains than any yet set forth. Ichang is about in longitude 112° 30′ East, while Hsing-lung-ch'ang is only about in 105° 30′ east longitude, a distance of about seven degrees or 480 miles further west. Hosie writes that the otter is used to drive the fishes into the net, but it works not outside the net but inside. Here follows his own statement of the *modus operandi:*

The net was circular and fringed with sinkers [*i.e.*, was a cast-net], and the fisherman, standing in the bows of the boat, casts his net with a semicircular sweep, covering a large surface of the water. The net disappeared, the fisherman holding on to a rope attached to the centre of the net, where there was a small circular opening. Drawing the rope gently

[8] Hosie, Alexander, "Three Years in Western China," etc., 2nd ed., London, 1897.

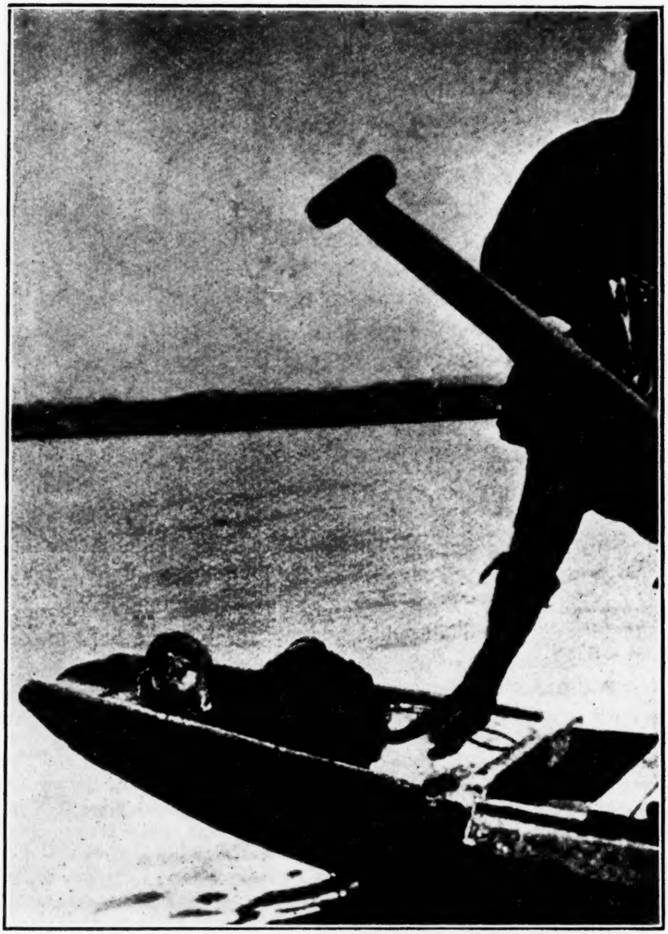
until the centre of the net appeared above the surface, he seized the otter, which was chained to the boat, and dropped it into the opening. After allowing the otter a short time to rout out the fish from the bottom and drive them upwards, net, fish, and otter were all drawn up together into the boat.

Navarra ("China und die Chinesen," Bremen, 1901, vol. II, p. 612) says that in many parts of China, but especially on the upper Yangtze, the otter is used. He avers that a cord is tied around the otter's neck to prevent his feeding and that he is then let down inside the net. Running around over the bottom the otter scares the fishes out of their hiding places and into the net. Then fishes and otter are all brought to the surface. The tying a cord around its neck to prevent feeding is a new process and one I believe not noted by any other author.

Now comes Gordon Moir (1909), last of all the authors cited for otter-fishing in China, but first in the matter of giving figures of the fishing otter. His six figures showing this use of the otter are all printed very dark and only the two which clearly present the otter are reproduced herein. His account[9] is herewith given *verbatim:*

There is only one place where that is practised, and that is at Ichang, about a thousand miles above Shanghai. At the present time there are not more than eight or ten fishermen who use the method. These men obtain the otters from streams in the neighborhood, one place being San-Yung-tung, about seven miles from Ichang. Each sampan or native boat employed in this kind of fishing carries one man, a casting net, and the otter, which has a collar with a light line attached to it. The casting net falls into the water in the shape of a cone, the apex being nearest the surface. The bottom is fringed with small pieces of lead, which tend to close the net on its being hauled up to the boat. On reaching a likely spot the fisherman gathers his net together with his right hand, and throws it out in such a way that the leaded bottom strikes the water in the form of a circle. The net is then allowed to sink. Whilst it is descending, the otter is moved towards the bow of the sampan, when it quietly dives outside the net. The little creature descending drives the fish before it towards the base of the net, and on arriving at the bottom it moves around, chasing the fish into the gaping mouth of the meshes. An interval of time is allowed to elapse, and the net is hauled up. The weight of the metal causes the lower part to be drawn together, thus enclosing the fish. The fisherman gives a tug with his left hand on the otter's line, and the animal, which

[9] Moir, Gordon, "Some Methods of Fishing in China," *Badminton Magazine*, 1909, Vol. 29, pp. 279–281, 2 figs.



FIGS. 1 and 2. Here the fisherman otter is resting from his labors, lying on the stern of his master's boat. In front of him is the net into which the otter drives the fish. These figures show the present day use of the otter in China, a use that goes back to 600 A. D. in the history of the one-time Celestial Empire. After Moir, 1909.

has remained outside the net, rises to the surface as the net is raised, and scrambles on board without aid.

Quite large fish are sometimes caught in this manner, some averaging four pounds. Occasionally, if there are no fish about, the otter will rise

to the surface and give the fisherman warning that a different place should be tried.

II—In Malaya

Undoubtedly the otter is used as a fishing agent in the Malay countries bordering on southern China, but unfortunately only two citations have been found. Theodore Cantor, in his "Catalogue of Mammalia Inhabiting the Malayan Peninsula and Islands" (*Journal Asiatic Society of Bengal,* 1846, vol. 15, p. 196), says that otters in his day and time were constantly used by the Malays in their river fishing. Also J. L. Kipling (to be quoted further on) says that they are so used in Cochin. Other than these two references, no data have come to hand.

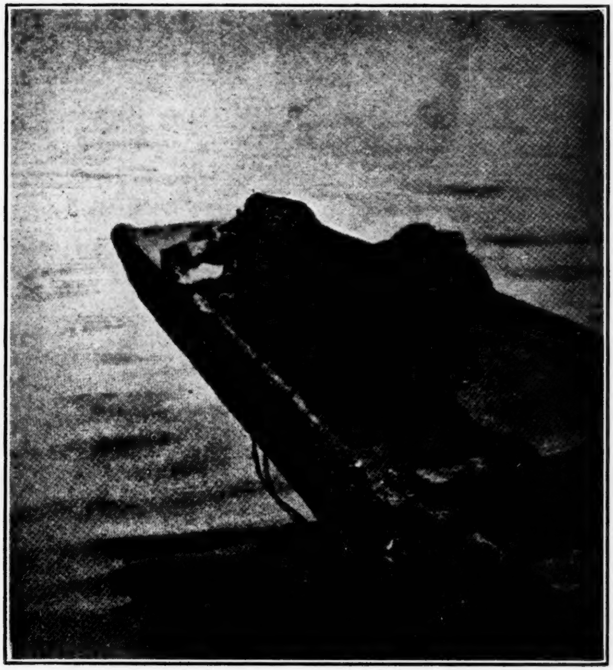


FIG. 2

III—In India

For India we have a fair number of references to this interesting use of the otter, due in part to the fact that this fishing method has long been in use there. Our first citation is to Bishop Heber,[10] who describes fishing otters not from "India's coral strand" but from the banks of the Matta Colly, a branch of the Ganges. Here is his very charming account of these interesting animals, the best given herein up to this point:

> We passed [near Dacca] to my surprise, a row of no less than nine or ten large and beautiful otters, tethered with straw collars, and long strings, to bamboo stakes on the bank. Some were swimming about at the full extent of their strings, or lying half in and half out of the water, others were rolling themselves in the sun on the sandy bank, uttering a shrill whistling noise as if in play. I was told that most of the fishermen in this neighborhood kept one or more of these animals, who were almost as tame as dogs, and of great use in fishing, sometimes driving the shoals into the nets, sometimes bringing out the larger fish with their teeth. I was much pleased and interested with the sight.

Bishop Heber's testimony for the Ganges region is confirmed by Jerdon[11] (1874). The young otters are often caught in the fishermen's nets, are easily tamed and trained to aid in fishing. Jerdon himself had a pet otter. In the Bhagalpur district of Bengal below Monghyr, where it is much used, C. J. O'Donnell[12] writes that "its success in killing and bringing up a fish, often five times its own size, is remarkable. Just outside the district of Rajmahal the fishing castes bestow much care in training otters."

The seaward front of the Gangetic delta, called the Sunderbunds, at the head of the Bay of Bengal is a swampy region intersected by creeks and channels which abound in fishes, fishermen and otters. And here the fishermen train the otters to catch the fish. So J. D. Hooker re-

[10] Heber, Bishop Reginald, "Narrative of a Journey through the Upper Provinces of India from Calcutta to Bombay, 1824–1825," 4th ed., London, 1829, Vol. III, pp. 157 and 162.

[11] Jerdon, T. C., "The Mammals of India," etc., Calcutta, 1874, pp. 87–88.

[12] O'Donnell, C. J., "Statistical Account of the District of Bhagalpur"; in W. W. Hunter, "Statistical Account of Bengal," 1877, Vol. XIV, p. 41.

lates in his "Himalayan Journals: Notes of a Naturalist in Bengal," etc. (London, 1855, vol. II, p. 339) that everywhere he found that the fishermen had tame otters to aid them in their fishing.

Other authorities vouch for otter-fishing in the Sunderbunds. So Hunter,[13] who says that the otters are tied to the boat by a rope and are trained to go overboard and play around the sides of the net to drive the fishes into it. Sterndale[14] likewise alleges the same thing for the same region. So also does Blanford.[15]

The trained otter is also made use of in the Indus River. Our first authority for this statement is David Ross, who is confirmed by W. T. Blanford (1888). Ross gives this intimate picture of the otter and its habits in his "The Land of the Five Rivers and Sindh" (London, 1883, p. 45):

> The otter (*Lutra nair*), or loodhra of the Sindhis, is very common on the banks of the Indus. These animals are trained by the Muhannas to catch fish, and also to drive them in shoals towards the nets, just in the same manner as a collie dog collects sheep at the order of the shepherd. The otters may be seen near the fishermen's boats in twenties and thirties, tied round the waist and secured to stakes, playing in and out of the water with the children and dogs.

The whole question of otter-fishing in India is summed up by John Lockwood Kipling (1891), who makes it clear that this use of the otter is not so widespread there as the preceding authorities would lead one to suppose. Quoting the ever popular "Natural History" of J. G. Wood that " . . . in every part of India trained Otters are almost as common as are trained dogs in England," Kipling[16] sets out the facts from personal knowledge as follows:

13 Hunter, W. W., "Statistical Account of Bengal," London, 1875, Vol. I, p. 302.

14 Sterndale, Robert A., "Natural History of the Mammalia of India and Ceylon," London, 1884, p. 155.

15 Blanford, W. T., "Mammalia" (in his "Fauna of British India including Ceylon and Burma," London [in parts] 1888–1891), p. 185.

16 Kipling, John Lockwood, "Beast and Man in India. A Popular Sketch of Indian Animals in their Relations with the People." London and New York, 1891, pp. 327–328.

But they are not used throughout Hindustan, nor in Central India, nor in the Punjab, where they are found in great numbers; and in the regions where they help in fishing they are never seen out of the hands of their owners, obscure river-side tribes. They are only employed in the back waters of Cochin, in part of Bengal, and on the Indus River. . . . They are effectively tamed in India, which is an easy matter, and they practice for the benefit of the fishermen the art to which they are ordained by nature . . . It is certainly interesting to see . . . the otters tethered to stakes near [the fishermen's house-boats], playing with the no less amphibious children and behaving like the playful, intelligent water-cats they are. But both this sight and the knowledge that they are used in this wise are distinctly *un*common and out of the range of the people of India at large.

B—Otter-Fishing in Europe

For this use of the otter in Europe there is quite a number of very old references, identical as to their allegations, but all indefinite as to the sources of the statements made. These are found in the old encyclopedias. The oldest on which I have chanced is in Vincent de Beauvais' "Speculum Naturale" (in two giant folios published at Strassburg *c.* 1480). In Vol. II, Liber XL, caput lxxxxix, is found the statement that the otter is sometimes tamed by the fishermen and trained so that he drives fishes into their nets as he rambles around over the bed of a stream.

An identical statement is found on folio 222 recto in the 1495 edition of the "De Animalibus, Libri Vigintisex" of Albertus Magnus. No source is given, but this is possibly copied from Vincent. The same statement in almost the same words is found in Johan von Cube's "Hortus Sanitatis" in Liber I, caput 89, Argentorati: 1536; in Conrad Gesner, "Historiæ Animalium, Liber Primus; De Quadrupedibus Viuiparis," Francofurti, 1620 (Section D, p. 685); Ulyssis Aldrovandi, "De Quadrupedibus Digitatis Viviparis," Bononiæ, 1637, p. 294; Edward Topsell, "The History of Four-footed Beasts," etc., London, 1658, pp. 445–446; and so late as 1856 by C. Knight in his "Pictorial Museum of Animated Nature," Vol. II, p. 219. No details are given, no authorities or experimenters are cited and, what is more regrettable,

no figures are given. Possibly all these accounts are echoes of Vincent.

IV—In Sweden

Of the European countries, the otter seems to have first been tamed and used for fishing in Sweden. Olaus Magnus, whose book contains so much interesting natural history data, gives the first account in 1555. Magnus[17] says (English version, 1658):

> But in Sweden with [*apud*] some great men they [otters] are made so tame, that when the cock [*sic*] gives them the sign, they will hop into the fish-pond, and bring forth a Fish of that bignesse he commands them; and then another, and a third, until he hath done enough as he was bid.

Magnus gives the first known figure of otter-fishing—reproduced herewith. Here the otter, filled with pride, is presenting a fine fish to the "cock," while in the stream nearby three other fish are patiently waiting to be caught.

FIG. 3. The trained otter brings a fish to the "cock," who has a pot over the fire ready to receive it. Overhead a bird (genus and species undetermined) filled with jealousy brings his contribution to the household larder. In the stream three other fishes are waiting to be caught.

From Olaus Magnus, 1555.

[17] Magnus, Olaus, "De Gentibus Septentrionalibus," Rome, 1555, Liber XVIII, Cap. xvi, p. 613, fig. Englished as "A Compendious History of the Goths, Swedes & Vandals, & Other Northern Nations," London, 1658, p. 183, fig.

FIG. 4. Another representation of the same scene from the Latin version of Olaus Magnus's book published at Basel, 1567.

Above is a bird which in emulation is also bringing a fish to the cook. This statement of Magnus's is quoted by the writers cited above but who postdate him, and by many others down almost to the present time. This same figure is slightly changed in the Latin edition, Basel, 1567. Both figures are reproduced herein.

Two hundred years later (*i.e.,* in 1755) Johannes Low published an account of a method used in Sweden for catching otters alive and training them to catch fishes. Various authors also give accounts of their methods—some as late as 1859. However, it seems best to postpone consideration of these data and bring all together in a separate section at the end of this article (p. 220). But before leaving Low, he must be quoted that a Baron Härleman reports that near Stockholm he had seen a trained otter go into a stream several times, and that it "each time had reappeared with a fine fish which it brought to its master." Also Low narrates that a Bengt Nilson, who lived in the northern part of Kristianstad in Sweden, had a trained otter which brought in so many fishes that his whole family was provided for.

From Low (1755) to Lloyd (1867), more than a hundred years elapse before another reference to otter-fishing in Sweden is found. Lloyd[18] gives the accounts from

[18] Lloyd, L., "The Game Birds and Wild Fowl of Sweden and Norway," London, 1867, p. 379–380.

Olaus Magnus and from Baron Härleman already quoted and concludes with a citation from a Captain Sven Littorin[19] concerning an otter which had been tamed and trained by a peasant that:

> It fulfilled the duties of a regular fisherman to its owner, and would often proceed to the river, where it captured quantities of large fish, salmon amongst the rest, which it brought untouched to the house, contenting itself with the refuse alone. Its master was thus never without fish at any season of the year, and in consequence sold his nets and other tackle, thinking them needless now that that he had so skilful a fisherman. From motives of jealousy, however, the poor animal was at length treacherously destroyed.

The next citation to this interesting practice in Norway is found in J. Bowden's "The Naturalist in Norway," etc. (London, 1869, pp. 72–73). Bowden refers in a general way to the method of training and says that when trained it may be used as a fishtaker by its master.

V—In Poland, Switzerland, France and Germany

Four scant references to otter-fishing in these four central European countries are grouped here before going to the British Isles, where the practice was common. The first is from Lloyd (ultimate source unknown) who relates that a Polish nobleman had a tame otter which guarded his stable and carriage house as a dog would do, but unlike most dogs would when ordered go to the lake, catch a fish and bring it to the house. It also went with him on shooting excursions and retrieved ducks which fell in ponds or marshes.

F. Tschudi, in his work "Les Alpes: Description Pittoresque de la Nature et de la Faune Alpestre" (Bern and Strassburg, 1889, p. 171), tells that alpine otters can be so trained as to go in the water at command and bring

19 I have sought in vain for works by Littorin and by Härleman in order to trace these accounts to their source. Even the catalogue of the British Museum does not list any books by Littorin, and while it does list two separate volumes of travels in the provinces of Sweden by Härleman, these works are not to be found in New York City nor in the Library of Congress.

to their masters' feet the fish that they catch. And Vanière[20] (1730) in Duncomb's metrical translation advises that:

> Should chance, within their dark recess, betray
> The tender young, bear quick the prize away.
> Tam'd by thy care, the useful brood shall join
> The wat'ry chace, and add their toils to thine;
> From each close-lurking-hole shall force away
> And drive within thy nets the silver prey:
> As the taught hound the timid stag subdues,
> Or o'er the dewy plain the panting hare pursues.

For Germany one account of this use of the otter has been found. An author who hides his identity behind the initials R. Z——r.,[21] writes that in the old days in Germany the otter was much used as an aid to the fisherman but that in modern times the practice has fallen into disuse. He tells that in his youth he knew an old hunter and forester on the edge of the Nürnberg forest who had a tame otter which fished for him and used to bring him pike and carp up to the weight of four pounds. He further narrates that he once borrowed the otter to catch fish for himself out of a nearby pond. He also knew another man, whom he suspected of being a poacher, who had a tame otter. He often watched this man fishing with the aid of his four-footed pupil and helper.

VI—In England

In a country where field sports are held in such high esteem as in England, it would be indeed surprising to find otter-fishing not practiced. As a matter of fact it was practiced there as late as *c.* 1880, while our earliest knowledge of this fishing dates back to 1618. In "Issues

20 Vanière, Jacques, "Prædium Rusticum" Tolosæ [Toulouse], 1730–translated by John Duncomb—"Fishing," London, 1809, and reprinted in W. B. Daniel's "Rural Sports," etc., London, 1813.

21 Z———r., R. Der Fischotter als Gehilfe beim Fischfang. *Oesterreichische Fischerei Zeitung,* Wien, 1908, 5. Jahrg., 490–493.

of the Exchequer,"[22] extracted from the official records of the Pell Office, one finds an item of payment, on October 10, 1618, to Robert Wood, "Keeper of his majesty's [James I's] cormorants, ospreys, and otters" of £66, 13s., 4d. for making fish ponds and for building a house in which to keep these fishing animals. Again, in August of the same year, a payment of £286 was made to meet similar expenses. It is well known that James I was fond of animals, that he maintained a menagerie and provided extensive hunting and fishing establishments—the latter having cormorants, ospreys and otters.

The next reference is found in Izaak Walton's "Compleat Angler" (1653).[23] In Chapter II, Piscator and Viator meet Huntsman, who is conducting an otter hunt. Huntsman had that morning killed a mother otter and had found her lair. To this he conducts the two and says: ". . . here's her young ones, no less then five: come lets kill them." But Piscator answers: "No, I pray, Sir, save me one, and I'll try if I can make her tame, as I know an ingenious Gentlemen, in *Leicestershire,* has done, who hath not only made her tame, but to catch fish, and doe many things of much pleasure." To this Huntsman answers: "Take one with all my heart, but lets kill the rest." The margin tells us that this "ingenious Gentlemen" was "Mr. Nich. Seagrave," and the next edition (1655) has his name set in the text in parentheses.

The next reference I have found to otter-fishing in England is to an author who is never suspected of dabbling in natural history and whose work on that subject is dismissed by his biographer in the Encyclopædia Britannica (11th ed.) with the merest two-line mention. Yet Oliver Goldsmith[24] compiled a work on natural history in

22 Devon, Frederick (Editor), "Issues of the Exchequer, being Payments made out of his Majesty's Revenue during the Reign of King James I. Extracted from the Records of the Pell Office," London, 1836, pp. 219–220, 333.

23 Walton, Izaak, "The Compleat Angler or the Contemplative Man's Recreation: Being a Discourse on Fish and Fishing," London, 1653, p. 44.

24 Goldsmith, Oliver, "A History of the Earth and Animated Nature." London, 2nd ed., 1779, Vol. IV, pp. 155–156. First ed., 1774, not seen.

eight volumes of such general interest that it has gone through at least twenty-five editions and was republished as late as 1881. After giving an account of the manner of training the otter for fishing (which will be considered later), he adds this point of personal observation, "I have seen one of these [trained otters] go into a gentleman's pond at the word of command, drive up the fish into a corner and seizing upon the largest of the whole, bring it off, in its mouth, to its master."

Thomas Bewick, in the second edition of his "General History of Quadrupeds," Newcastle upon Tyne, 1791 (first edition, 1790, not seen by me) knew of a number of instances of otters trained to fish for their masters and cites the specific case of a William Collins living near Wooler in Northumberland who had such a trained otter. Once on a fishing excursion, the otter got lost but after several days was found, and when restored to its master gave extravagant expressions of its joy. Another man found his trained otter "very useful in fishing, by going into the water, and driving trouts and other fish towards the net."

Daniel ("Rural Sports," London, [1801] vol. I, pp. 518 and 520) refers in a general way to the fact that the otter can be tamed and taught to fish for its master either by bringing the individual fishes to him or by driving the fish towards the nets.

Bell in his "History of British Quadrupeds" (1st ed. London, 1837, pp. 134–135) refers to the domestication, training and use for fishing of the otter, quotes a large number of the European authorities above cited but unfortunately adds nothing new, and hence needs no further citation here.

F. H. Salvin[25] (1859), the well-known trainer of falcons, also tried his hand at the training of otters, of which he

[25] Salvin, F. H., "Training the Otter for Fishing"—in Freeman, G. E., and Salvin, F. H., "Falconry: Its Claims, History, and Practice," London, 1859, pp. 350–352.

almost always had one or more on hand and sometimes a brood. How successful his efforts were may be judged from the following account of the habits of such a trained animal:

In 1848 I succeeded in taming a young otter, which I called "Diver," so perfectly, that he would follow me into the country like a dog, and jump into my lap to sleep. At first he was an awkward swimmer, his early education being defective, owing to his separation from his parents, and I found it was necessary to be cautious with him, as cold water at first produced fits. Knowing that otters can scent fish under water, and even smell eels, etc., when in the mud, I taught him to dive by sinking meat with a plumb-line, which he never failed in finding. As the otter cannot eat a fish of any size when swimming, it *must* come to land to do so; its master must then approach it quietly, and taking hold of its long and strong tail (called by otter hunters "the potter"), hold him with one hand, whilst he takes the fish from him with the other, immediately rewarding him with small pieces of fish, after which he will again take the waters in search of more. Otters are particularly fond of salmon, and in some waters a great many may be taken. I need hardly remark that the death-struggle of a large salmon with his foe, in a rapid stream, is a grand and exciting thing to witness.

H. S. Thomas, the authority on sport in India, in his admirable book, "The Rod in India," (2nd ed. London, 1881), in writing of the tame otter (pp. 259–268), quotes at length from various authors but especially from F. H. Salvin in *Land and Water* (no definite citation given) and from his extract I quote in part as follows:

. . . my object, is to try and describe a glorious battle, which came off on the 21st instant, between a trained otter and a very large pike. I was summoned to the scene of action by the otter's master, Mr. Hulse, of the Rifle Brigade, who brought it from India about a year since. The pond where the fish was is a small but deepish one in Stoke Park, near Guildford. The otter, following its master to the place, entered the water and immediately dived, when we could follow his track as he hunted below by the long string of bubbles ("bells," as otter hunters term them), which, coming from his nose, marked his passage. In a short time there was no doubt as to "a find," as the rush and troubled state of the surface too plainly indicated, for it was like two express trains in full chase of each other. All this lasted but a short time, say, about half a minute, and the exertion and coldness of the water, etc., seemed to take a good deal out of the animal, for he not only came up to breathe, but landed, and after

rolling himself, which they delight in doing, "time being up," in he went again at the word of command. Many rounds like this took place, the pike always breaking away, until it was varied by the capture of a carp, the head of which he was allowed to eat. His appetite seemed whetted by this, for he became very eager, and, whenever he came across the pike, a great struggle took place, but the big fish seemed such a monster that he could not worry him, yet, by the aid of his feet, he turned him over once, but never brought him to the top, though the otter's tail often waved above water. Up to this time behind the fish's head was the part attacked, his great and powerfully armed jaws being avoided, but now the fish was evidently growing weaker, and the otter changing his tactics by attacking the enemy in the rear. Each round told in favour of the otter, and, finally, "the sponge was thrown up" by the beaten fish being towed to land by its tail, amidst the loud and hearty whoo-whoo-ops! of all present, the doubtful battle having lasted above half an hour. The fish, which proved to be a female, weighed 20 lbs. 11 ozs., and the weight of the otter (a female) and very like an English otter, is only 18 lbs. Thus ended as well-contested a battle as I ever witnessed, and a sight I would have gone any distance to have seen.

VII—In Scotland

In a rough mountainous country like Scotland, abounding in torrential streams which provide salmon and trout for the food of and many hiding places among the rocks for such semiamphibious animals as otters, one would expect to find these latter in numbers. They do abound and they have been used for fishing. The earliest reference is to Martin Martin,[26] who says of the Hebrides or Western Islands that "the Amphibia of these Isles are Seals and Otters in abundance; some of the latter are trained to go a Fishing, and fetch several sorts of Fish home to their masters." And there is little reason to doubt that this method of fishing was also practiced on the mainland of Scotland.

The next definite account is given by Thomas Bewick (1791), who, in the work previously cited, gives the following incident:

Some years ago, James Campbell, near Inverness, had a young Otter, which he brought up and tamed. It would follow him wherever he chose;

26 Martin, Martin, "A Description of the Western Islands of Scotland" London, 1703, p. 341. Second ed., London, 1716—reprinted London, 1884.

and, if called on by its name, would immediately obey. When apprehensive of danger from Dogs, it sought the protection of its master, and would endeavour to fly into his arms for greater security. It was frequently employed in catching fish, and would sometimes take eight or ten salmons in a day. If not prevented, it always made an attempt to break the fish behind the fin next the tail; and as soon as one was taken away, it immediately dived in pursuit of more. When tired it would refuse to fish any longer; and was then rewarded with as much fish as it could devour. Being satisfied with eating, it always curled itself round and fell asleep; in which state it was generally carried home. The same Otter fished as well in the sea as in a river, and took great numbers of codlings and other fish. Its food was generally fresh fish, and sometimes milk.

Another person, who kept a tame Otter, suffered it to follow him with his Dogs. It was very useful to him in fishing, by going into the water, and driving trouts and other fish towards the net.

Daniel, in the "Supplement to Rural Sports" (London, 1813, on p. 55), relates that a young man at Lochside in the parish of Blair Gowrie tamed a young otter so that: "It follows his Master where he desires, obeys his command, accompanying him to the Locks [*sic*] and Rivers in the vicinity, where it dives for Fish, brings them to land to his Keeper, and returns in search for more."

John McDiarmid gives two interesting accounts of fishing-otters which seem worthy of quotation. They are found on pp. 136–137 and 142–143 of his "Sketches from Nature" (Edinburgh and London, 1830). They read as follows:

I have been assured, however, by a clergyman in Galloway, that there was an otter in Dalbeattie, within the last few years, which purveyed extensively in the same way. Its mistress was a poor widow woman, and the otter, when led forth, plunged into the Urr or the neighbouring burns, and brought out all the fish it could find. The widow rewarded it well for its trouble, and carried the surplus home to her young family. As an animal so tractable must have been exceedingly useful, I regret to add that it was crushed to death one day by the weight of some domestic utensil it unfortunately upset, while scrambling for food.

Since writing the above, I have been reminded of another tame otter, the manners of which I was requested to describe in February, 1827, by Norman Lockhart, Esq., Lanarkshire. Some time in the beginning of that year, my informant paid a visit to his friend, Mr. Monteith, of Carstairs, and while about to depart, was surprised to see a curious animal issuing from the dog-kennel, and anon running about the wheels of his carriage, when called on by the appropriate name of "Neptune." This circum-

stance naturally led to some inquiry, from which it appeared that the otter was caught in the spring, 1825, when only a few days old, and actually suckled by a pointer bitch! At first it was as wild as the Corsbie cub, but afterwards it became so tame and domestic, that the gamekeeper was induced to take it under his especial patronage. And undoubtedly the man had good reason for so doing. As the purveyor of game, he could do little without his faithful canine allies, and the otter's services were found equally useful in another way—that is, in procuring a dish of excellent burn trout, when the nature of the weather or season was such that the finny people refused to rise, whether tempted by bait or fly. In a state of nature, otters merely fish for themselves, but when fairly civilized and properly looked after, they appear to act on the principle of the clergy, contenting themselves with a tithe or so of the fruits.

Few writers on the natural history of the Scottish Highlands have had a more exact knowledge and few have written more charmingly than Charles St. John. In his "Natural History and Sport in Moray" (Edinburgh, 1863), on p. 284, he speaks in general of otters trained for fishing and adds the following account, of which he had personal knowledge since its happenings occurred in his own community. It may also be found on p. 266 of the second ed. (1882) of the above work. Mr. St. John writes that:

Mr. John Cumming of Altyre caught a young otter at the Findhorn [River] one day in spring, about half grown. He thoroughly tamed him, keeping him constantly by him, and in a short time trained him to catch trout, taking sometimes above a dozen in a forenoon out of the small stream near the house. His general food was porridge and milk, which he devoured quite as freely as fish. This most interesting pet was unfortunately killed through the neglect of a keeper after Mr. Cumming went to Ceylon.

VIII—In America

That the American otter can be and has been tamed is attested by considerable evidence. This need not be given here, but for admirably described instances the reader is referred to Vol. II, pp. 9 and 10 of Audubon and Bachman's "Quadrupeds of North America," wherein are set forth accounts known personally to the authors. Actual accounts of its use as a fisherman are confined to two, one for each of the Americas.

Peter Kalm (for whom our beautiful shrub, the mountain laurel, *Kalmia,* has been named) travelled from September, 1848, to October, 1851, in the eastern parts of North America (*i.e.,* in Delaware, Pennsylvania, New Jersey, New York and in the St. Lawrence section of Canada) and wrote up his experiences in an interesting book.[27] In this he says of the otter: "I have seen some which were as tame as dogs, and followed their masters wherever they went; if he went out in a boat, the otter went with him, jumped into the water, and after a while came up with a fish." In the same paragraph he says of the allied form, the beaver, that: "Beavers have been so tamed, that they have gone on fishing, and brought home what they had caught to their masters." These two citations are found in a section devoted to accounts of *ferae naturae* which had been tamed by the settlers.

The following extract is given from an article "Florida Otter Pets," by Minnie Moore-Wilson, in *Forest and Stream,* 1898, Vol. 51, p. 84. "The otter in a domesticated state is easily taught to fish for his master, and to retrieve to land, for in bringing captive fish to shore he is only following his natural inclinations." Whether this is a matter of personal observation, or even a Florida happening, cannot be said since the context gives no help.

The one South American record of the use of the otter for fishing is given by the traveler, Harry L. Foster, in his book, "The Adventures of a Tropical Tramp," New York, 1922, p. 242. At Bermudez, Peru, east of the Andes: "One man had a baby otter. . . . The owner explained to us that he had only begun to feed it fish; when it grew up a little older, he said he would teach it to go into the river and catch fish for him, thus returning his kindness."

[27] Kalm, Peter. "En Resa til Norra America," etc., 3 vols. Stockholm, 1753–61. "Travels into North America, Containing its Natural History," etc. (John Reinhold Forster, translator), 2 vols., London, 1772, Vol. I, pp. 162–163.

THE TWO USES OF THE FISHING-OTTER

Merely to put the matter in categorical form, it may be stated here that in all the countries where the otter is or has been extensively used as a fisherman, in China, in India, in Scandinavia and in the British Isles, it has been used in two ways—to catch the individual fish and bring it to its master or to drive the fishes into the net. These two uses parallel those for dogs, as shown by the present writer in another paper.[28]

HOW THE OTTER IS TRAINED TO FISH

It may be said at once that all descriptions of the methods used in taming and training otters are by Europeans, and thus our investigations into this matter are strictly limited. One would expect in the accounts of otter-fishing in China to find descriptions of the methods of the training, but such are entirely lacking, even in such firsthand accounts of Chinese fishing methods as Dabry de Thiersant's.

For reasons which will become apparent later, our study of the methods of training otters in Europe will be carried on in reverse chronological order. The most recent account comes from Norway, the neighboring country to that in which the earliest descriptions of the proper method originated. J. Bowden, in his "Naturalist in Norway," etc. (London, 1869, pp. 72–73), gives the following very incomplete directions:

> The otter . . . may be tamed . . . When sufficiently tamed, it may be taught with an artificial or even a dead fish; should it injure the fish, it must receive a gentle castigation with a whip. When it knows how to dive in pursuit of a fish in the water, it should be sent in to catch fishes for its master.

Captain Salvin, the well-known trainer of cormorants of the forties and fifties of the last century, also tamed

[28] Gudger, E. W., "Dogs as Fishermen," *Natural History*, 1923, Vol. 23, pp. 559–568. 3 figs.

and trained otters. His account of the activities of his trained otter "Diver" may be found on page 215. Concerning the taming he writes that:

> An otter which it is intended to tame should be taken young, and confined in a yard well secured over both the top and sides with wirework, containing a pond, a shed with dry straw facing the sun, and a hollow trunk of a tree into which he may creep and rub himself, as they delight in doing after swimming.
>
> The otter trainer must be careful to observe the various cries of the animal, in order not to irritate its temper as it has three distinct modes of expressing its feelings. Thus when pleased it whistles, when suspicious of danger it blows through the valves of its nose, when vexed it growls. It is, therefore, only advisable to play with it when it shows itself to be amiable by its whistling. Otters are particularly playful after feeding, and it is quite a pretty sight to see them play with a ball, for even on land their activity is wonderful.

Bell (1837, work cited) gives more careful and explicit directions as follows:

> They should be procured as young as possible, and they are at first fed with small fish and water. Then bread and milk is to be alternated with the fish, and the proportion of the former gradually increased till they are led to live entirely on bread and milk. They are then taught to fetch and carry, exactly as Dogs are trained to the same trick; and when they are brought to do this with ease and docility, a leather fish stuffed with wool is employed for the purpose. They are afterwards exercised with a dead fish, and chastised if they disobey or attempt to tear it; and finally, they are sent into the water after living ones. In this way, although the process is somewhat tedious, it is believed that the Otter may certainly be domesticated and rendered subservient to our use.

This account agrees very closely with that found in Alexander Fraser's "Natural History of the Salmons, Herrings, Cod, Ling," etc. (Inverness, 1883, pp. 84–85). Moreover, in all the various editions of J. G. Wood's "Natural History" an almost identical account is found. Now these writers must have copied each other or their accounts must have a common source. The former is possible, the latter is certain, for investigation shows that this common origin for all these accounts is to be found in Goldsmith's "History of the Earth and Animated Nature" (2nd ed., 1779). Then the question be-

comes "Where did Goldsmith get his data?" He himself answers this by saying that it comes from "the account given us of this article by Mr. Lots, of the Academy of Stockholm." Now so far as I know there was no such person as Mr. Lots, but there was a Johannes Low (previously referred to), and careful comparisons of his article and of the account in Goldsmith's book proves beyond any doubt that in Low's article we have the original source of all these accounts of taming and training the otter.

This article by Low is so important historically, so explicit as to details and so interesting in that it is the only one provided with figures of the implements used that it seems well to reproduce it fully. After giving directions for the capture of the young by driving them out of their burrows by means of dogs and sticks into a net stretched across the exit, he says:[29]

When one succeeds in taking a young living otter like this, it must immediately be put under guard. For a few days it should be given fish to eat and water to drink, after which the water should be diluted more and

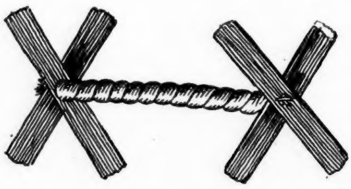


FIG. 5. The implement, made of straw bound with leather and having at each end wooden cross pieces, which the otter at word of command is taught to fetch and carry. After Low, 1752.

[29] Low, Johannes, "Sätt at fänga uttrar lefvande och invätta dem, at bära hem fisk" Kongliga Svenska Vetenskaps Academiens Handlingar, 1752, vol. 13, pp. 139–149. This whole set (40 vols.) of the publications of the Swedish Academy, 1739–1779, was translated into German and published at Hamburg and Leipsic, 1749–1783. In this the citation to Low is—"Eine Art, die Fischottern lebendig zu fangen, und sie abzurichten das sie Fischen bringen." Königlicher Schwedischen Akademie Abhandlungen, 1752, vol. 13, pp. 139–149. The article was deemed so important that it was also translated into Dutch in Uitgezogte Verhandlingen (Amsterdam) in 1757, and into Latin in Analecta Transalpina at Venice in 1762.

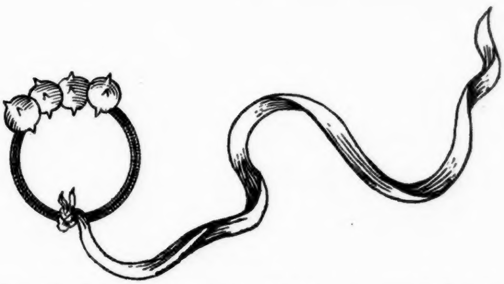


FIG. 6. The "halter" with its rein which is put around the otter's neck. When the rein is held taut the spikes prick the otter's neck and bring him to a halt. When held loosely the pricking ceases and at the word the otter goes forward. After Low, 1752.

more with milk, broth, cabbage or peas. As soon as the otter will eat these things undiluted, fish must be given to it very infrequently, bread being substituted for these. This is quite enough to nourish the animal. Finally, the otter must never get a whole fish or the viscera of a fish. It should only have the head.

While the otter is being taken care of in this way (which should be done in a room where there is a number of people) one must try to make it as tame as possible. This will be practicable in a short time.

Next one makes an apparatus out of straw, bound with sail twine or leather . . . and of a thickness to enable the otter to close its jaws over it. On either end two short rods are placed cross-wise, as shown in fig. 3 of plate 4. Next one takes a thin band on which four or five balls the size of nuts have been fastened. In each ball four spikes are set at intervals. This is all illustrated in fig. 4. This band is put around the otter's neck and fastened at the nape. Bound to this knot is a thong a couple of "Ellen" long.

After all this has been done as directed, one must train the otter so that she obeys willingly; so that when a certain command is given, for example "Come here," and when at the same time the thong is given a strong pull, she comes quickly and obediently. Then one takes hold of the otter, puts a hand in the band at the nape of the neck and twists it until she opens her jaws. As soon as this happens, one puts in front of her the above mentioned apparatus and cries suddenly, "Lay hold." As often as the otter lets go, one must twist the band until she holds the apparatus fast. Then one must call "Let go" and twist until she does so. Thus one proceeds until the otter lays hold and lets go at the word of command.

Thereupon one lays the straw implement on the ground, where there must be no sand; pulls on the cord in the manner stated above; pushes the otter's head down; pulls the otter to the apparatus with one hand and holds this with the other. At first, one pulls the apparatus away from the otter,

finally, however, bringing it to her so that upon the outcry "Lay hold," she holds it fast.

One proceeds in this manner until the otter takes hold of the implement on a very slight pull of the long cord; so that one first shouts "Come here" and pulls the apparatus gently to the otter, and then "Let go" and gently takes it from her. When one has finally accomplished this, and the otter goes quickly after the apparatus when it is thrown, then one can throw, instead, a handkerchief or a glove. At last, when the otter is willing to fetch anything without being called or compelled, one can then throw it something that it likes to eat. It must, however, be forced, by the use of the cord, to bring this object back again. The thing should not be heavy. One can in this way train all animals, at least those that can be handled, to fetch things.

After the otter brings back everything that it can lift, and everything that it has been sent after, then one should take it to a clear and not too deep body of water, carrying with one a small, dead fish, and a rather large live one. One first throws the dead one in, for the otter will without doubt take this willingly. As soon as this happens, however, one should make the otter give up the fish. Finally, the live fish is thrown into the water and the otter holds fast to it without difficulty. As soon as the otter brings the fish out of the water, one gives it the head to eat.

This is not entirely clear, but it is the best that can be made out of this old German. That this method works, Low avers by citing the experience of Bengt Nilson given on page 210 of the present article. Low states, however, that old otters are trained with great difficulty and urges that the young only be used if possible.

The writer, R. Z——r., whose account of fishing with the otter in Germany has been given above, also describes the method of training formerly used in that country. He states that otters three or four months old are at the best age for the training to begin, and that if cared for well they are available for use for fifteen or sixteen years. He recommends a milk and cereal diet with fresh vegetables and fruits and finally cooked meat—all at the temperature at which they come to the master's table. Raw meat or fish and blood should never be given the otter, since one wants to train it to fish for its master and not for itself—to get it away from its predatory nature. Specifically as to the method of training, our author says:

To train it for fishing one first lets it fast for one or two days until it gets very hungry, and then places a freshly cooked hot fish before it. The

hungry animal will at once sink its fangs in the fish and will get burned. If this is repeated a few times, it will forever afterward have a proper awe of biting into scaly creatures. The thoroughly trained animal that has, as I have already mentioned, learned to fetch and carry like a dog, will quickly learn to carry a leather and oakum imitation, or training fish, without biting it at all, and once so far along, it will not be hard to train him to bring the fish and give it to his master. When the otter has progressed to this point on land, where he will bring this imitation fish and give it up to his master, then one can begin to let him carry real dead fishes and then live fishes, on land. If he does this, then one has him bring dead fish out of the water, a big pool, or basin, and then live ones. If he cuts his burden, then one repeats the manoeuver with the hot cooked fish, or punishes the otter in which, most remarkably, beating is much less effective than sousing with water. As much as the otter loves the water, he has a peculiar dread of being sprinkled or having it poured on him. Before one takes the otter along for real fishing, one lets him get hungry, gives him a fine meal and only then takes him to practical work. If the animal is really well filled, it naturally follows that he will not be so apt to bite the fish he catches.

Naturally, the young otter does not learn all this on the first day. But with patience and perseverance in training, you will find yourself well rewarded and in a short time, just as is the case with most young dogs.

THE POLYCHAETE ANCESTRY OF THE INSECTS. I. THE EXTERNAL STRUCTURE[1]

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Two general hypotheses exist relative to the evolution of insects. The one is the Crustacean theory of Müller (1864), Haeckel (1866), Wood-Mason (1879) and others who have maintained that the insects have evolved from Crustacean forms resembling the immature "Zoaea" stage where there were three pairs of mouth parts and three pairs of walking appendages corresponding to those found in insects. Modifications of the Crustacean theory have been presented by Handlirsch (1903, etc.), who holds that insects originated from Trilobite ancestors, extinct forms placed as an aberrant group of Crustaceoidea by most systematists, and by Crampton (1918, etc.), who believes that the insects have arisen from forms similar to the Anaspidacea or Mysidacea, small Crustaceans of primitive structure.

The other interpretation is the Campodean theory of Brauer (1868, etc.), which derives the insects from the "Myriapoda"—the Chilopods in the strict sense—and the Onychophoroidea by way of campodeoid forms. This is on the basis of the resemblance of the larvae of many orders to the existing Campodea, a genus of apparently primitive insects belonging to the Thysanura. It is the latter theory that has received the approval of the greater number of systematists who have taken an interest in problems of phylogeny.

That there is quite another interpretation of the origin of insects indicating their descent neither from the Chilopods and the Onychophorans by way of *Campodea,* from the Trilobites, or from the generalized Crustacea, but directly from the Polychaete Annelids, is my decided opinion. This I would term the Polychaete theory.

[1] Contributions from the Samuel Mather Science Hall. Biology (Ser. 31). No. 1.

Such a view I earlier presented (1913) in a brief discussion concerning the relationship of the parapodium of the Polychaetes to the various areas of the maxilla and other appendages of the insects. The direct derivation of the insects and their allies from such an ancestral type permits the explanation of many characters not easily accounted for on any other basis. While Mayer (1876) advocated the origin of the insects from an annulate worm, which eventually developed ventral and "possibly" dorsal appendages, the implication was that they were newly developed, no suggestion being made of any correspondence between the parapodia and the appendages of the insects. The particular point that Mayer had in mind was in establishing the numerical relationship between the segmental organs of the hypothetical annulate worm consisting of eighteen segments which he assumed to be the ancestor of the insects, and the spiracles taken together with the malpighian tubules of the insect. The conclusions formulated in this connection, however, were so severely criticized by Brauer (1878) that, whatever merit may have existed in the work, it was soon forgotten, except as the historical "Archentomon theory."

The body of the typical insect so far as the evidence is available at the present time consists of twenty-two segments, provided one accepts the existence of a post-mandibular segment bearing the appendages termed the superlinguae. On the basis of the specialization of the segments in groups it has been customary to speak of the cephalic region, the thoracic region and the abdominal region of an insect. In the head region and in the abdominal region, however, a secondary grouping of segments has taken place so that one may with propriety state that an insect is a heterometameric organism formed from five homometameric segmental groups. These groups consist of a prestomal area of three segments, a poststomal area of four segments, a thoracic area of three segments, an abdominal area of seven segments and a caudal area of five segments.

Efforts to arrive at a conclusion as to the structure of a typical segment of the insects acceptable to those interested in their embryology and morphology have not met with pronounced success. The difficulty is due to the wide diversity of form exhibited by the various orders of insects, the pronounced differentiation of the segmental groups mentioned, together with the inability to agree on the ancestral form from which the insects and their allies, the Symphyloidea, Chilopoidea, Pauropoidea, etc., have arisen.

It is to only one particular phase of the question that I here wish to call attention, namely, the relation of the pleurites and the appendages of the thorax in the insects to the parapodia of the Polychaete Annelids, for it is in the thorax, I am inclined to believe, that one finds the most generalized part of the body so far as the external structure is concerned.

The pleural or lateral part of each thoracic segment consists of two sclerites, the episternum and epimeron, names given by Audouin (1824) in his study of *Dytiscus circumflexus* Fabr., the large water beetle. The origin of these pieces has received little attention, although several explanations have been offered. None of these explanations seems to me to be adequate.

Miall and Denny (1886) suggested that the pleurites as represented by the episternum and epimeron belonged to the lateral area of the segment so far as they were present in the insects, but that in the cockroach they could be considered basal parts of the leg adherent to the thorax. Inasmuch as even the constancy of the two pieces was doubted throughout the insects in general, it is evident that their relation to the base of the leg was looked upon as a specialized condition present in the Blattidae alone. Banks (1893) believed that the two pleurites were to be accounted for through the fusion of two primitive segments, a theory which I myself was earlier (1900) inclined to accept, but which I have long considered untenable. Crampton (1909) suggested that the two areas

were "due to a mechanical stress," apparently forgetful of the heresy thus implied in connection with the inheritance of acquired characters. Snodgrass (1909) concluded that the apparent division between the areas resulted from the development of a ridge which was needed to strengthen the pleural area as a support to the leg. The more recent papers devoted to the anatomical structure of the insects by Berlese, Börner, Bugnion, Crampton, Feuerborn, Franz, Göldi, Handlirsch, Heider, Heymons, Imms, MacGillvray, Verhoeff, Weber and others present no new interpretations.

In this paper it is my purpose to call attention to some of the evidence that has induced me to believe that the ancestral type from which the insects and their allies have developed belongs to the Polychaetes, and that intermediate forms will eventually be found in the rocks of the Cambrian or Silurian periods. The well-preserved fauna of the Burgess Shales belonging to the Middle Cambrian of British Columbia, which Walcott has noted in a series of papers, is of decided interest in this connection.

The general argument as to the Polychaete ancestry of the insects may be stated most advantageously in connection with a series of diagrams illustrating the course that evolution has taken, on the basis of the hypothesis advanced.

First, let us consider the structure of the external parts in a typical segment of a living Polychaete (Fig. 1). The epidermal cells underlying the integumental covering have secreted a thin protective cuticula with no pronounced folding except in connection with the slightly marked secondary annuli, which at times are marked off by transverse furrows. The later development of a pronounced segmentation, as it takes place in the various groups descended from the annelids, closely parallels the phyletic development of the notochordal area of the vertebrates, which like the insects and their ancestors have passed from an aquatic to a terrestrial environment.

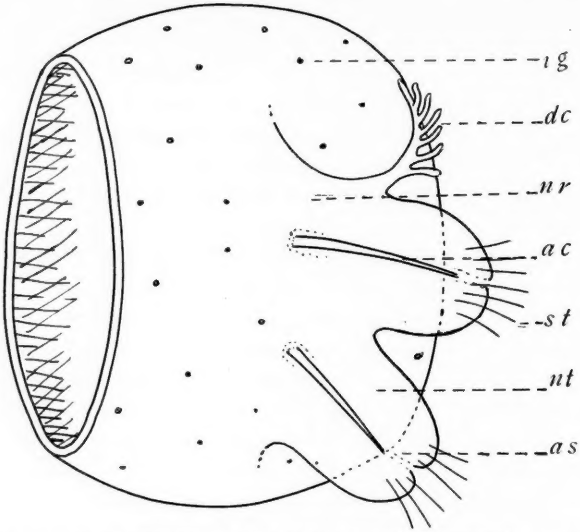

FIG. 1. Typical segment of a Polychaete Annelid illustrating the parapodium and its structure.

ac = aciculum.
as = acicular sack.
dc = dorsal cirrus.
ig = integumentary glands.
nr = neuropodium.
nt = notopodium
st = parapodial setae.

In the Polychaetes the striking characteristic of the segment is the development upon each side of a lateral fold called the parapodium, which propels the organism through the water and along the sea-bottom. It is attached in a plane nearly perpendicular to the longitudinal axis of the body and consists of a dorsal branch (*nt* = notopodium) and a ventral branch (*nr* = neuropodium). There is also a dorsal appendage (*dc* = dorsal cirrus), generally developed as a sensory organ, but often forming a gill or more rarely a protective sheath called an elytron. Occasionally other dorsal as well as ventral cirri, usually of smaller size, are present. The dorsal and ventral branches of the parapodium are each supported by a large thick seta (*ac* = aciculum) enclosed in an integumentary sack (*as* = acicular sack), while groups of small setae (*st* = setae) are found at the distal extrem-

ities of both the notopodium and neuropodium. The openings of epidermal glands (*ig* = integumentary gland) are scattered over the surface as outlets for the integumentary glands.

There are only a few changes that need to take place in the position and form of the parapodium to convert it

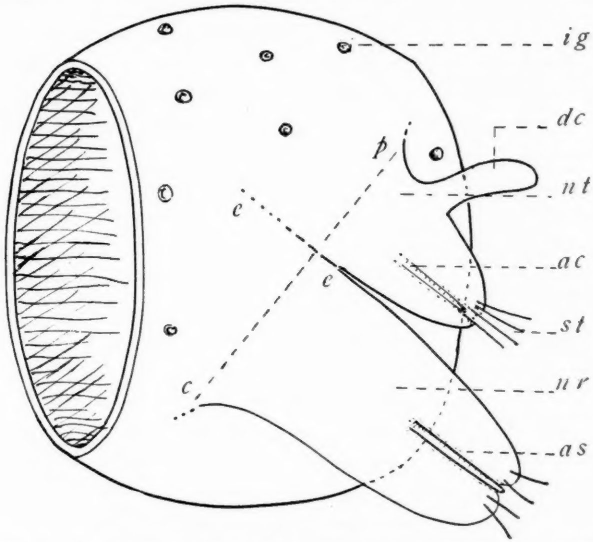

FIG. 2. Typical segment of a Hypothetical Polychaete Annelid intermediate between the living Polychaetes and Insects.

ac = aciculum.	*ig* = integumentary gland.
as = acicular sack.	*nr* = neuropodium.
cp = coxo-pleural suture.	*nt* = notopodium.
dc = dorsal cirrus.	*st* = parapodial setae.
ee = episterno-epimeral suture.	

into the typical structure of the appendage with the pleurites of the insect. These changes may be indicated by a hypothetical segment (Fig. 2) intermediate in form between the segment of a typical Polychaete and a typical insect. The parapodium has moved ventrally and forms a plane which in its relation to the axis of the body has turned clockwise nearly forty-five degrees. The lower branch (*nr* = neuropodium) has become large and some-

what elongated as compared with the upper branch (*nt* = notopodium) which remains short and small. The large cirrus (*dc* = dorsal cirrus) retains its development, while any ventral cirri that may have been present have disappeared, unless we assume the retention of small basal cirri which eventually developed as the propteron and pteron (wing). The integumentary glands (*ig* = integumentary gland) assume an increased size and function correlated with the semi-aquatic environment of the organism and become restricted in number.

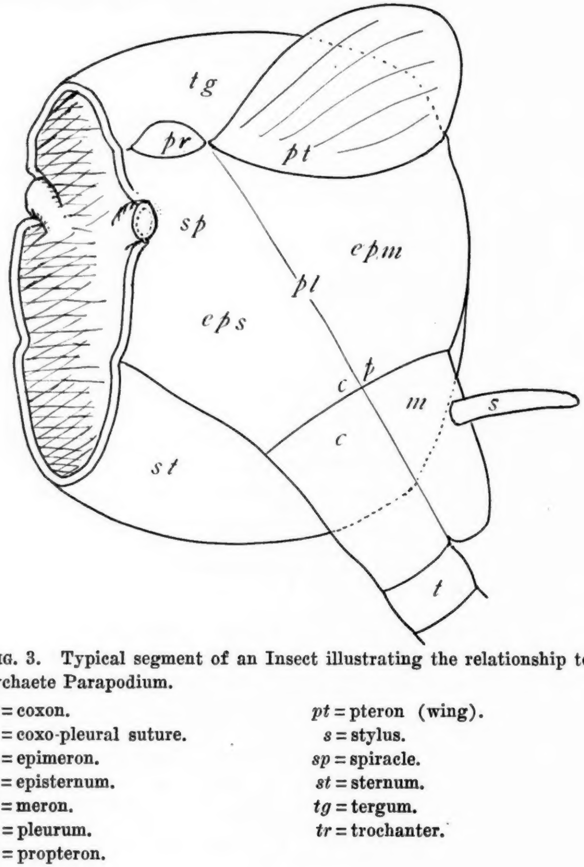

FIG. 3. Typical segment of an Insect illustrating the relationship to the Polychaete Parapodium.

c = coxon.
cp = coxo-pleural suture.
epm = epimeron.
eps = episternum.
m = meron.
pl = pleurum.
pr = propteron.
pt = pteron (wing).
s = stylus.
sp = spiracle.
st = sternum.
tg = tergum.
tr = trochanter.

It is a result quite consistent with the ecological conditions under which many of the Polychaetes existed in marshy areas of the coastal regions. The parapodia would more and more be compelled to support the body of the individual as it moved through the shallow and partially dried pools. The subsequent changes, including that of aerial respiration through the development of the integumentary pockets as tracheal openings, compared to that which has taken place in *Peripatus* and allied genera, are infinitely less than the changes that have occurred in the descent of the terrestrial vertebrates from aquatic forms.

There are many of the existing Polychaetes in which the structure of the parapodium is closely in accord with the form noted and to which attention will be called in a subsequent part of the present paper.

In turning to a discussion of the external structure of the insects, let us first consider a typical segment (Fig. 3) with reference primarily to the chitinous skeletal system, for it is here that the relationship with the Polychaetes is most apparent. The segment consists of a dorsal area (*tg* = tergum), a lateral area (*pl* = pleurum) and a ventral area (*st* = sternum). The pleural area is formed from two pieces, of which the one (*eps* = episternum) occupies an anterior ventral position, while the other (*epm* = epimeron) is found on the posterior dorsal part of the pleurum. The appendages are the leg formed from the "coxa," which in turn is composed of an anterior ventral piece (*c* = coxon) and a posterior dorsal piece (*m* = meron), and an evaginated sack-like part of the integument forming the wing (*pt* = pteron). Anterior to the wing is a sclerite (*pr* = propteron) which from its tracheation in certain cases has apparently developed in a way similar to the wing, and which from its constancy in the various orders of insects is here included as a typical part of the segment. A large seta-like appendage (*s* = stylus) is attached to the meron (Machilidae) of the meso- and meta-coxae as well as to the ster-

nal abdominal coxae in many of the Apterygotes. Tillyard advises me that the stylus is segmented in some of the New Zealand Machilids. On the anterior margin of the pleural area is the integumentary opening (*sp* = spiracle) of the trachea.

Many secondary areas have developed in the insects and the groups allied to them. Among these are to be noted the trochantin, ante-coxal piece, subdivisions of the sternum, tergum, episternum, epimeron, propteron, etc. Included in such areas I would place the micro-thorax of Verhoeff, present not only on the anterior margin of the prothorax but also upon the mesothorax, metathorax and abdominal segments in *Campodea, Japyx,* etc., and comparable with similar areas among the Chilopods, as in the Geophilids, etc.

It seems quite obvious that the areas termed "primary" may all be developed from the Polychaete segment, and that the correspondence between the parapodium and the pleural area and basal parts of the leg in the Hexapods indicates a definite relationship. With the parapodium turning on its axis, as indicated in Fig. 2, the proximal part coalescing with the pleural part of the segment and the ventral branch becoming elongated and eventually segmented as it attains a ventral position supporting the body, there is, I feel certain, an explanation of the origin of insects much more satisfactory than any of the theories thus far advanced.

It will be well to discuss somewhat more explicitly certain details in connection with the typical structure of the segment among the insects which bear upon the solution of the problem.

In the suggestion that the basal part of the parapodium has fused with the lateral area of the segment to form the episternum and epimeron, there is really nothing extraordinary. A phyletic development of a similar nature has taken place among other insects, and is particularly noticeable in the family Dytiscidae of the Coleoptera where the metacoxae have the form of expanded plates

immovably fused with the sternum. Furthermore, as Haase (1889*b*) has pointed out, each abdominal sternite in the insects represents a pair of coxae that have fused with the sternum so that all trace of the sutural region is lost in most forms.

The division of the pleurum into two areas is not at all confined to the thorax, as some would have us believe, but is to be noted in head region as well as in the abdominal region of many insects. Thus, as I have pointed out (1913), the cardo at the base of the maxilla is composed of two pieces which I there termed the endocardo and the ectocardo on the basis of their apparent correspondence to the neuropodium and notopodium of the parapodia. These two pieces, I am inclined to believe, represent the episternum and epimeron of the thorax. Even among many of the Chilopods, where there has apparently been a secondary breaking up of the pleura into numerous sclerites, there are still two principal areas demonstrable in each pleurum. Snodgrass (1909) has called attention to this characteristic.

The anterior portion of the coxa, as noted in the accompanying drawings, I have termed the coxon. This is the area which I earlier called the coxa genuina and which has been mentioned by later writers as the eucoxa and the coxa vera. While from certain standpoints it may be considered unfortunate that a priority principle does not enter into anatomical nomenclature in the strict sense that it exists in systematic work, a mononomial is here certainly to be preferred to a binomial term, and the word coxon, while open to objections from the classical side as is also the hybrid "eucoxa," possesses the merit of brevity as well as a relatedness to the terms meron and coxa.

Whether an attempt to reduce the confusion of anatomical nomenclature in the insects by presenting new terms for typical generalized structures is justified will remain for future students of the anatomy of insects to decide.

The stylus attached to the meron represents, I am inclined to believe, a dorsal cirrus of the Polychaete parapodium, although two other possibilities present themselves—the one that it is the modified distal area of the notopodium with the terminal tip composed of setae formed from the notopodial aciculum, while the other is that it represents the development of a small setae and is wholly of a secondary character, as Haase (1889*a*) has suggested. The explanation on the basis of a modified notopodial cirrus, which in the different segments has evolved into the maxillary and labial palpi, the mesothoracic and metathoracic styli (Machilidae), the abdominal styli of many Apterygotes and in all probability the tracheal gills of the Ephemeridae, etc., as well as the cerci of the caudal segments, seems better in accord with the facts as I have already suggested (1913). Furthermore, on such a basis one might explain the paired eversible sacks of the abdominal coxae in many Thysanurans as modified integumentary acicular sacks of the notopodium and neuropodium which in most forms had become reduced to a single sack through fusion or suppression. In the single case known where there are three sacks on a "coxa," some of the sacks if actually separate would have to be accounted for as secondary. These suggestions, however, relate to problems which are beyond the scope of the present paper and for their solution demand a larger background of embryology and morphology than exists at the present time.

The dorsal appendages of the segment as represented in Fig. 3 consist of an evaginated sack forming the wing here designated as the pteron, and the area anterior to its base, which from its constancy throughout the insects both on the mesothorax and on the metathorax is included as a part of the typical segment and termed from its position the propteron. Like the wing it is a hollow segment where structurally large enough to examine and in all probability has similarly developed as an integumentary outpushing. Various names such as pterygo-

dum, parapteron, tegula, squamula, etc., have been applied to it on the different segments in various orders of insects, and it might seem that less confusion would result from the retention of some of these names. While the term pterygodum of Latreille (1820–22) has priority, it was used in a restricted sense for the part at the base of the mesothoracic wing in the Lepidoptera and is rarely noted in the literature relating to the insects. The more familiar term, parapteron, was first used by Audouin (1824) to designate a supposed sclerite which he believed to exist on the anterior margin of the mesepisternum of *Dytiscus circumflexus* Fab. This was merely an area bounded posteriorly by the articulatory ridge at the point of junction with the prothorax, extending in many Coleoptera entirely across the sternum. The transfer of the term to the pieces in front of the wing (propteron) arose in connection with a footnote attached by Audouin to a translation of a paper by MacLeay (1832), where Audouin suggested that the piece termed the squamula in the Hymenoptera was homologous to the parapteron, which he had noted in *Dytiscus*. Consequently, the term parapteron really has no standing.

The patagium of the prothorax corresponds, I am inclined to believe, to the mesothoracic and metathoracic wing, and similarly possesses a propteron. To one familiar with the embryos of certain of the termites as well as with the structure of the prothorax in many fossil insects, the reasons for such a conclusion will seem obvious.

The problem of the origin of the wings still remains a difficult one. That they do not correspond to the tracheal gills seems certain, particularly when one takes into consideration the relative position of the gills, the coxosternum, the pleurites and the metathoracic coxae in a young Ephemerid. The presence of the episternal and epimeral areas, assuming that the parapodium furnishes an interpretation of the origin of the pleurum, might lead to the assumption that a basal notopodial as well as a basal neuropodial cirrus had become changed into an elytral

scale-like formation receiving tracheal branches and had given rise to the wing and propteron. The structure of *Worthenella cambria* Walcott, a middle Cambrian annelid with the apparent biannulate division of the segments as subsequently figured (Fig. 4), is interesting in this connection. The theory of the origin of the wings, as proposed by Müller (1875), namely, that they are developed from the expansion of the tergum, seems to be untenable, although it is the one which has generally been accepted. Nature has a tendency in evolution to modify existing organs rather than to develop new structures, and I would here consider such a tergal expansion with its new articulation and wing muscles a new structure.

The position of the spiracular openings on the anterior margin of the segment is quite consistent with the parapodial development of the pleurum in that the scattered respiratory pockets of the integument, reduced in number to the paired segmental spiracles with their ramifying trachea, would tend to occupy a position outside of the parapodial area, either anteriorly or posteriorly, although a secondary migration might occur. This seems to have been the case in some of the Chilopods, notably the Geophilidae. We would here hold to the opinion that the spiracular openings have developed from numerous irregularly disposed integumental glands of the Annelids, as suggested, I believe, by von Kennel, and that the reduction and subsequent segmental arrangement parallels that which has taken place and is still exhibited by existing forms of the Onychophorids.

The development of the transverse segmentation in the parapodium to form the boundaries between the episternum-epimeron and the coxon-meron, as well as the coxon and trochanter, etc., would be correlated with the increasing chitinization of the integument and the need of mechanical assistance from the walking appendages, by the individual. Such seems to have been the history of segmentation among the Vertebrates, Echinoderms, Molluscs, etc., both in the primary and the secondary axes

of the body. In other words, the need of pronounced articulatory surfaces is correlated with the development of firm unyielding areas, such as bone, chitin, etc.

The large acicular setae of the neuropodium, often biuncinate distally, furnishes a part that may have readily become transformed into the tarsal claws. Some evidence for such a change is afforded by one of the fossil Polychaetes mentioned later.

Two forms of extinct Polychaete Annelids found by Walcott in the Burgess Shales of the Middle Cambrian Period near Field, British Columbia, are of much interest

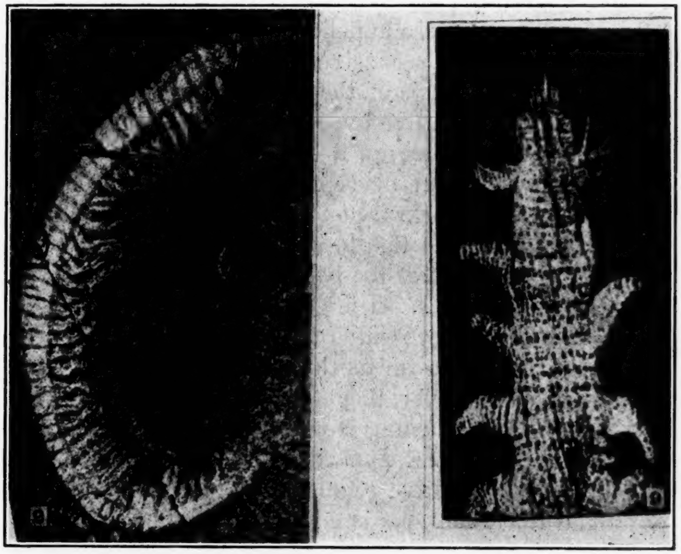

FIG. 4. *Worthenella cambria* Walcott. (Left) A Polychaete Annelid from the Middle Cambrian with parapodia developed as two extremely elongate lobes. (From Walcott, 1911, by permission.)

The only individual known consists of about 46 segments and is 60 mm in length. It existed approximately 250,000,000 years ago. It is interesting in possessing parapodia similar to those demanded by a type intermediate between existing Polychaetes and Insects.

FIG. 5. *Aysheaia pedunculata* Walcott. (Right) A Polychaete Annelid from the Burgess Shales of the Middle Cambrian, British Columbia. Illustrating the hook-like setae at the end of the parapodia and the integumentary pits. (From Walcott, 1911, by permission.)

in connection with the parapodial theory of insect evolution here presented. The specimen to which the name *Worthenella cambria* Walcott (Fig. 4) was applied in the paper by Walcott (1911) is represented by a single individual about 60 mm in length, having some forty-six segments. Two striking characteristics are observable, one in the much elongated and apparently bilobed parapodium and the other in the division of the segment into two secondary annular areas, as observed dorsally. The eyes and the appendages of the head leave no question as to the Polychaete nature of the specimen, although, as Walcott correctly suggests, it belongs to none of the existing families of these annelids.

If we attempt the reconstruction of a typical segment of *Worthenella* (Fig. 5) on the basis of the available data, there are two alternative hypotheses which one may consider. The one appearing to me as the most consistent interpretation is that of representing the parapodium turned somewhat clockwise on its axis so that the lobular division extending to the dorsal margin of the segment forms a continuation of the boundary separating the secondary annular areas. It is possible, of course, that the annular groove is not related to the biramose division of the parapodium. So far as the outline of the parapodia are concerned, however, they are folded in such a manner that the clockwise turning is indicated. The other interpretation is that the apparent segment represents a fusion of two primitive segments, as in existing Diplopods, and that each lobe is a distinct parapodium. One would not expect such a specialization, however, in an evolutionary stage where the comparatively thin cuticula was quite sufficient to take care of the contortions of the individual. A distinct segmentation followed by segmental fusion belongs to a later phyletic period.

Another form found by Walcott which must also receive consideration in any discussion of the evolution of the insects and the classes allied to the insects is *Aysheaia pedunculata* Walcott (Fig. 5) also from the Bur-

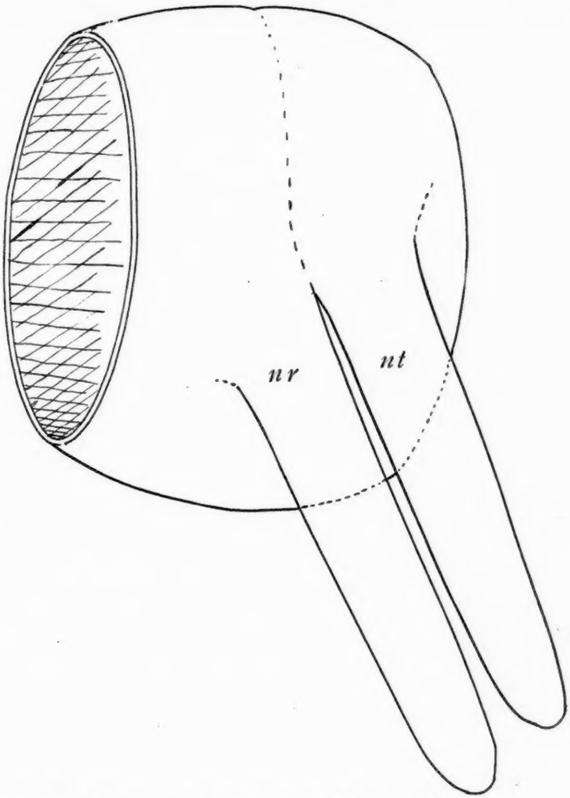

FIG. 6. *Worthenella cambria* Walcott (Polychaeta). A reconstructed typical segment illustrating the probable position of the parapodium.
nr = neuropodium. *nt* = notopodium.

gess Shales. The parapodia possess terminal "hook-like and straight setae" and closely resemble the ambulatory appendages of existing Onychophorids where the terminal claws have undoubtedly developed from similar hook-like setae. That the tarsal claws of the insects have had a similar development seems extremely probable, although a different line of descent is indicated from that of *Peripatus* and its allies where the appendage has developed from a simple and not from a biramose parapodium.

Among existing Polychaetes the relation of the various areas of the parapodium to the pleurites in the appendage of the typical insect is illustrated in many forms. Thus in *Eulepis splendida* Treadwell (Fig. 7) a marine form described from Porto Rico by Treadwell (1901) the

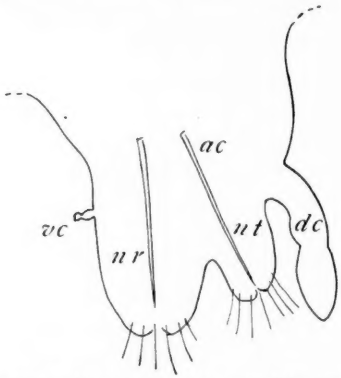

FIG. 7. Posterior Parapodium of *Eulepsis splendida* (Polychaeta) Treadwell, Porto Rico. Redrawn from Treadwell, fig. 21.

ac = aciculum sack.	*nr* = neuropodium.
as = acicular sack.	*nt* = notopodium.
dc = dorsal cirrus.	*vc* = ventral cirrus.

neuropodium is much larger than the notopodium, a functional development which as already noted appears to be correlated with the swimming and creeping mode of progression. The dorsal cirrus is prominent and has a position about midway between the basal and distal part of the parapodium.

In *Anthostoma latacapitata* Treadwell (Fig. 8), another Polychaete from the same region, a similarly relatively large neuropodium is to be found although the dorsal cirrus is less prominent and relatively more attenuate. Treadwell does not figure the dorsal and ventral aciculus, although their position is to be inferred from the form of the parapodium.

In reference to existing insects a few representative forms taken from different orders will serve to indicate the structural relationship with the typical segment pre-

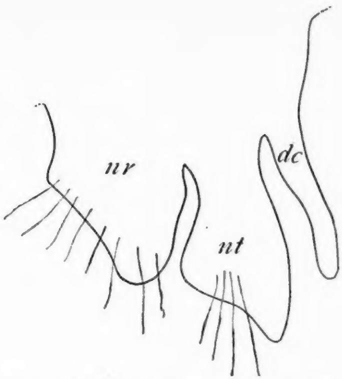

FIG. 8. Parapodium of *Anthostoma latacapitata* Treadwell, Porto Rico. Redrawn from Treadwell, fig. 62.

dc = dorsal cirrus. *nt* = notopodium.
nr = neuropodium.

sented in the preceding part of the paper and with the parapodium as illustrated in fossil and in existing Polychaetes.

The Mecoptera, more familiarly known as "scorpion flies," form a small but an extremely interesting phyletic group of insects, as has been pointed out by Tillyard (1920). The mesothorax of *Panorpa communis* (Fig. 9), with its anterior episternum-coxon-trochanter-femur area and its posterior epimeron-meron area, presents a structural arrangement easily to be derived from the elongate biramose parapodium of a form not far removed from the Middle Cambrian *Worthenella cambria* Walcott. The general transformation so far as the external integument is concerned is completed through the shortening of the notopodium, the fusion of the base of the notopodium and neuropodium with the lateral part of the segment, and the development of the segmentation of the parapodium, as indicated, form the corresponding segmentation in Panorpa. The position of the wings is in accord with their possible derivation from basal cirri, as earlier suggested. Basal cirri are present in many existing Polychaetes, and the small "oval scale-like objects" to which

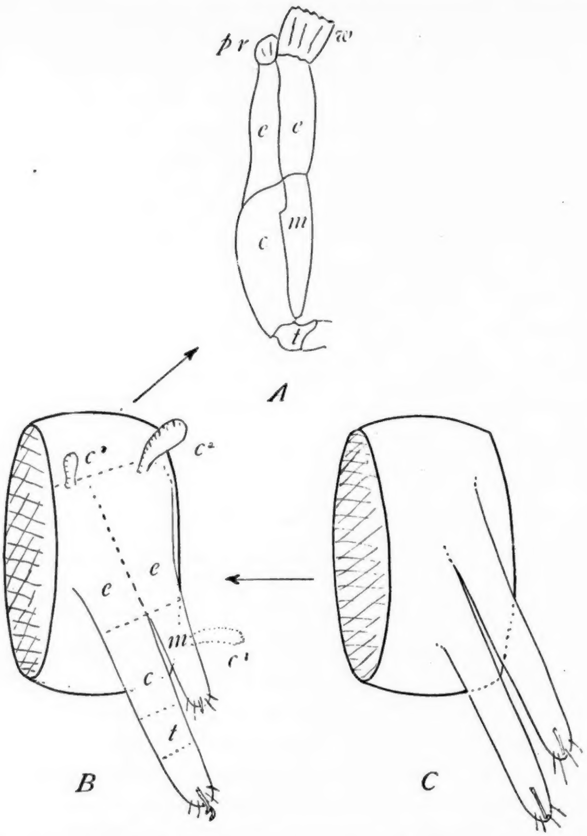

FIG. 9. (A) *Panorpa communis* (Neuroptera), metathorax showing wing, pleurites and coxa. (B) Segment of hypothetical Polychaete intermediate between *Panorpa* and (C) *Worthenella*, a fossil Polychaete from the Middle Cambrian.

c = coxon.	*nr* = neuropodium.
c′ = cirri.	*nt* = notopodium.
ee = episternum-epimeron.	*pr* = propteron.
m = meron.	*t* = trochanter.

Walcott (1911) calls attention in the shale surrounding the impression of Worthenella may have something to do with the problem. Here again one must await additional material which will throw light upon the subject.

In the Lepidoptera the arrangement of the various areas as illustrated by *Cossus cossus* (Fig. 10), one of the large moths, is not far removed from the similar areas as represented by the typical segment of the insects. Two developmental changes are to be noted, the first of which may, however, represent a more primitive condition than exists in other orders, namely, the extreme development of the propteron to form the so-called tegula or para-

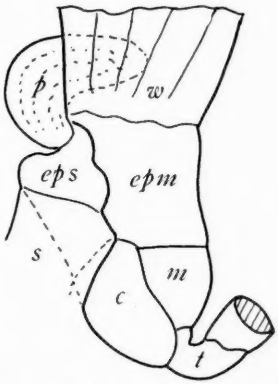

FIG. 10. *Cossus cossus* (Lepidoptera). One of the large moths illustrating the bifurcate nature of the pleurites and coxa in the mesothorax. The sternum has partially grown over the episternum.

c = coxon.	*p* = propteron.
epm = epimeron.	*s* = sternum.
eps = episternum.	*t* = trochanter.
m = meron.	*w* = wing (pteron).

pteron at the base of the mesothoracic wing. The second change exhibits the tendency of the sternum to extend in a posterior lateral direction over the episternum, so that the latter is apparently cut off from the coxon. Such a development is present in many other representatives of the insects.

The Coleoptera, as represented by the metathorax of *Harpalus calignosus* Fab. (Fig. 11), do not at a casual glance indicate any pronounced similarity with the arrangement of the sclerites as shown in the typical segment. This is largely due to the dorso-ventral compres-

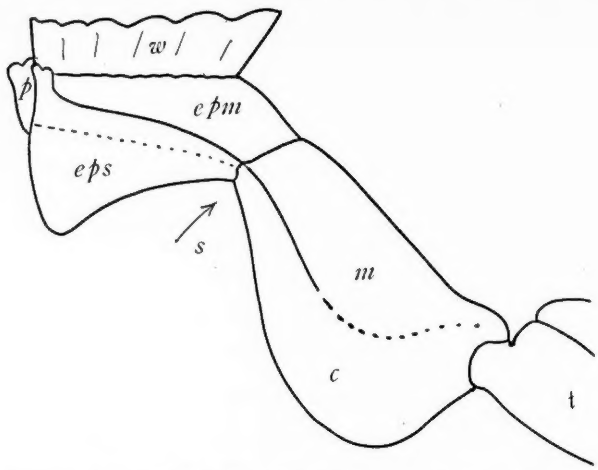

FIG. 11. *Harpalus calignosus* Fab. (Coleoptera). Metapleurites from left side with wing attached. Illustrating the parapodial type of structure.

c = coxon.
epm = epimeron.
eps = episternum.
m = meron.
p = propteron.
s = sternum.
t = trochanter.
w = wing.

sion of the body with the resulting distortion of the parts. The tendency of the sternum to develop as in the Lepidoptera is particularly noticeable, while the coxal groove for the reception of the femur, particularly characteristic of the metacoxae in the Coleoptera, tends to render the coxon-meron suture obsolete, particularly at the distal end.

Many other representatives of the insects or of the Chilopods or the Symphylids could be noted where the same typical form is indicated. In representatives of the Apterygote insects, like *Machilis, Campodea, Japyx* or in the Protura, the pleurum-appendage area apparently represents a more specialized development of the parapodium than in the Pterygote insects. To those who have long held to the opinion that the "Thysanurans" are representative forms from which the winged insects have evolved, the implied conclusion will seem a heresy. While

it is true that one finds many characters in the Machilid type which are evidently of a primitive nature and that definite relationships with such Symphylids as *Scolopendrella* and *Scutigerella* are clearly indicated, it is by no means necessary to insist that the winged insects have developed from such a type. The aerial life which they lead in general has permitted the retention of the cylindrical body and at the same time the parapodial structure. Insects without wings, as well as many of those with wings which need protection by leading a terrestrial life as opposed to an aerial existence, have become much flattened dorso-ventrally and the pleurum correspondingly modified. The pleural regions of the Thysanurans as well as the thoracic regions of the Coleoptera, the Blattidae, etc., illustrate this.

The evidence presented, fragmentary as it is, appears to point definitely to the conclusion that the various groups of insects and their allies have evolved directly from the Polychaete worms, and that the parapodium is the fundamental structure from which not only the appendages and pleurites of the thorax but also the appendages and pleurites of the cephalic and caudal regions have developed. Furthermore, there is evidence in favor of the theory that the wings have originated from basal parapodial appendages quite different in position from those modified as tracheal gills in existing insects. From the systematic side one therefore concludes that the Annulates form a definite phylum, the Annularia, consisting of a series of classes among which are the insects and their allies, and that the Arthropods are wholly an artificial group. We may enumerate these classes as the Pterygotes, the Thysanurans, the Collembolans, the Proturans, the Symphylids, and the Chilopods. More remotely related to the insects are the Diplopods, the Pauropods and the Onychophorans.

In order to eventually establish the course of evolution among the insects paleontological material must be procured. The extremely well-preserved forms, such as

Worthenella, Aysheaia, etc., obtained by Walcott from the Burgess Shales of British Columbia, indicate that it is here that efforts to obtain such material should be made and that transitional forms between the Polychaetes and the various classes of "Arthropods" are certainly to be found in the Cambrian or Silurian rocks.

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FACTORS IN PHYLOGENETIC DEVELOPMENT

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I

THE question of phylogenetic development has so long involved conflicting theories of method and controversial treatment of those theories that it is difficult to select a title or open a discussion of the subject without reference to the familiar terms "inheritance of acquired characters" and "germ-plasm theory" or "continuity of the germ-plasm." These terms and the theories which they represent have been important in the crystallization of scientific thought on the subject of evolutionary method, and are still useful as an indication of the major tendencies of our literature on the subject. They are unfortunate in that they emphasize the differences, rather than the essential harmony, between the various components of organic existence, and thus lead us away from fundamental considerations by the attractive fabric of evidence which each has brought to its support.

The last few years are interesting and fortunate in this connection, for they have concentrated the thought of scientists on the question of evolution, through various agencies, more than at any time since Darwin's epochal life, and have brought keenly to our attention the need for progress in our knowledge of the method of evolution. The old order no longer arouses solely partisan support of one or the other side of the controversy, but an increasing doubt of the value, even the soundness, of such treatment, and a realization of the indeterminate status of the entire question.[1, 2, 3] The beautiful clarity with which Eldridge[4] points out the unproved state of the

1 McClung, Cowdry's "General Cytology," p. 614, 1924.
2 Eldridge, "The Organization of Life," 1925.
3 Detlefsen, *Physiological Review*, V, 244 *et seq.*, 1925.
4 *Loc. cit.*

widely supported Weismannian theory is a valuable addition to the field, although by no means new.[5] The more partisan contributions of recent years are no less important, for they are largely of a nature to force upon the scientific world a more logical attitude toward the possibility of the inheritance of acquired characters, so-called. It is a notable fact that fields which draw attention to long phylogenetic series and to the intimate association even in apparently minor details of the organism and its environment, such as paleontology and entomology, respectively, have aroused in many a belief in the potency of the environment in the shaping of organisms, even in the absence of any well-formed theory of method.

The importance of the question need scarcely be urged upon scientific readers. Inheritance, the precious freight of the germ-plasm, is obviously permanent within all demonstrable limits, insofar as it concerns this question. The human race alone exerts a marked control over its environment and that of other organisms. Granting the intelligent direction and constant application of a given influence, can the two factors act together, or must they remain forever separate, the one all-powerful, the other impotent? Can man expect, as a result of the many things he does for himself, an improvement in his remote descendants or must their inheritance be determined by some unknown force acting in the germ-plasm? It is not a simple problem, and many pages could be filled with even a brief analysis of its intricate ramifications among the known fields of science. However, all problems of biology must involve fundamental truths and some fundamentals of this problem appear to have been obscured by the prevailing controversial treatment.

II

As has been said, the ideas of germinal continuity and the inheritance of acquired characters have had a certain

[5] Baldwin, "Development and Evolution," p. 35, 1902, expresses similar ideas.

value. We can not doubt that the individual organism is, to a certain extent, a definite entity. Nor can we doubt that certain of its characters are inevitably a result of stimuli received from its environment. Reminders of the inseparability of these factors in the existence of any organism are too numerous to require citation, but for the purposes of this analysis it is necessary to bear in mind at once their essential distinctness and their inevitable association. The organism is whatever its inheritance determines from the moment of fertilization, yet without its environment it can not realize even its inherited possibilities. The environment, on the other hand, is wholly incapable of influencing the organism in any significant way without arousing it to active response.

Weismann brought vividly before the scientific world the possible continuity of a heritage, once established, and emphasized the ability of the germ-plasm to produce, over and over again, independent of external influence, the characters of the species. Of course if the egg becomes too hot or too cold, or if it be exposed to an unfavorable chemical stimulus or the wrong kind of light rays, it fails to develop, but a hen's egg can not be expected to produce anything but a chick, and one does not plant an acorn to raise a maple tree. Weismann and his followers have, however, failed to establish the source of the changes which have obviously come about in organisms as completely as their opponents have failed to establish the transfer of somatic modifications to the germ-plasm. The idea of the continuity of the germ-plasm is well established, but there is no reason to believe that his interpretation of it is of value. In the development of the organism a wonderful succession of changes occurs, leading from zygote to alimentary tract, to integument, and among all the parts of the body, to other germ cells like those from which it sprang. This succession is sometimes very definite, and from generation to generation it constitutes, of course, continuity. We can not establish its discontinuity in any single case, for even in animals

capable of a remarkable degree of regeneration, the removal of the reproductive organs results in failure to reproduce, even though the lost parts essential to individual existence may be regenerated.[6] Only by going low enough in the animal kingdom to find a low degree of differentiation do we find regeneration accompanied by a continuation of sexual reproduction, and in such cases there is no real proof of interruption of the normal continuity.

In the plant kingdom the extreme cases of production of complete flowering plants from fragments of leaf or root are again suggestive, although inconclusive, but here in the common repetition of agamic reproduction generation after generation, as well as in animals where the same phenomenon is found, there is a parallel condition of great significance. In begonias, for example, or in the roses, peonies, irises and other plants of modern gardens, and in such animals as sponges, *Hydra* and some flatworms we can trace a potentially unlimited continuity of any tissue in the body from generation to generation. In brief, continuity is apparently not an indication of isolation, nor yet of insulation from the somatic tissues, but a phenomenon merely incidental to the reproductive function of the germ-plasm. Organisms which reproduce wholly by the sexual process inevitably show it to a conspicuous degree. Father and son may indeed be chips from the same block, but a chipped block is likely to show marks of the axe.

The fundamental nature of the germ-plasm is therefore an open question. The science of genetics emphasizes the importance of the chromosomes as carriers of the heritage, and apparently with good reason, although not without opposition.[7] The remarkable series of orderly changes in cell reproduction and gametogenesis, in which the accurate repetition of chromosomal transformations is not approximated by the cytoplasm, together with

6 Morgan, "Regeneration," p. 9, 1901.

7 Ritter, "The Unity of the Organism," II, 1919.

other evidence adduced in support of this theory, seems to be reasonable proof that the chromosomes are the chief, if not the only carriers of hereditary characters. The evidence of cytology testifies that they are also the common essentials of the germ cells. Not only this, but they are also said to be the same in all cells of the body.[8, 9] The mere fact that mitosis is apparently a means of accomplishing equal nuclear division would lead to the latter conclusion, since cleavage after cleavage is seen to occur by mitosis during ontogeny, with equal distribution of the chromosomes. Inquiry into the fundamental nature of the germ-plasm thus becomes resolved into an inquiry into the fundamental nature of its chromosomes, and since they must be looked upon as similar to those of other cells of the body, into an inquiry into the nature of chromosomes in general.

Chambers[10] gives an interesting account of the behavior of injured cells which demonstrates that a nucleus can not live without its cytoplasm, any more than an enucleate cell can carry on all of the processes of its normal life. Cell reproduction also demonstrates the universal association of the two parts, for cytoplasm gives rise to cytoplasm and nucleus to nucleus. That they are essential to each other and that interchange goes on between them is abundantly proved, so that the cell as a whole is indeed the unit of living matter as it now exists. It is a significant fact that of this inseparable pair the cytoplasm undergoes great differentiation in the development of the different tissues and organs of the body, while the nucleus goes on indefinitely dividing its chromosomes equally between daughter cells, and in gametogenesis accomplishing an even more remarkable separation and reassociation, without showing evidence of more than very minor differentiation. The part played by the nucleus in this process of cytoplasmic differentiation has

[8] McClung, *op. cit.*, p. 609 *et seq.*

[9] Hance, *Biol. Bull.*, LI, 443, 1926.

[10] Chambers, Cowdry's "Cytology," p. 237 *et seq.*, 1924.

been looked upon as open to question, but that it does play an initial part of great importance, and a controlling part during the life of the cell, is the only view compatible with our knowledge of cell behavior, even though we can not say how the association is effected.

As we consider the functions of living matter both in the individual and in the comparison of different organisms, we can not fail to note that while it has certain general properties, it also shows a striking tendency to distribute these properties more or less completely among specialized cells in the complex individual. Coordination, a general power of protoplasm, is delegated in large part to the nervous system. Movement, also a general power, becomes the function of the muscles. By retracing this path of specialization as illustrated by existing animals we come to the undifferentiated cell, wherein living matter is at its simplest. Thence over uncharted seas of speculation we arrive at several hypotheses of the origin of living matter. If there is any vestige of reason or logic in these hypotheses, one thing must be looked upon as axiomatic, *viz.*, that the cell itself is a specialization, and that it was once derived from undifferentiated living matter, which must necessarily have possessed the fundamental properties of its modern derivatives. The differentiation of this primitive substance, through means unknown, must have involved as a fundamental step the production of the two parts of the cell which are now universal in their occurrence, the nucleus and cytoplasm. In all cases differentiation is for the effective accomplishment of specialization. While the functions realized by the cytoplasm through its differentiation are varied, the functions of the nucleus apparently consist only of its controlling activity in the cell, and the important part which it plays in heredity. To these considerations may be added that wherever a differentiated tissue or differentiated cells occur in the complex body, they retain the characters of their kind; through the coordination of the body they receive such substances and such stimuli as

they can use, regardless of their immediate material surroundings. Thus elastic fibers have the same properties in the walls of an artery as in the reticulum of the spleen, and skeletal muscle in the esophagus as in the foot.

By applying these principles to the chromosomes, we may interpret them as a specialization of living matter so remote in origin that it is now essential and universal in occurrence, whose function is to bear hereditary qualities of the entire organism and to bring them to expression in the differentiated cytoplasm. As such a specialized substance we may conclude that the coordination of the body maintains them in the same state wherever found.

III

Of the environment, which constitutes the other great factor in the determination of the qualities of organisms, little can be said which is not already well expressed in print. We recognize that every organism has an association with the surrounding world, from which it receives stimuli of a chemical or physical nature as well as the materials of which its body is composed, and to which it responds through simple tropisms or more complex reactions. By this intricate relationship and the ultimate return of the substances which it has used during its life, every organism contributes to the complexity of the environment of every other organism; the trees shade other plants and so modify their relations to the light, while the deer is pursued by the wolf, in a relationship which accounts for various characters of both. The environment thus becomes twofold, the inorganic and the organic, each of which is complex in itself.

These things are true of all organic life, whether simple or complex, but in their relationship to simple organisms they become most striking. In a dense culture of Protozoa, for example, such as the mass of *Colpoda* sp. in a jar before me as I write, each individual has an association with the water in which it lives, its temperature,

hydrogen-ion concentration and the amount of light which it transmits, as well as the wave length of that light. In addition it is associated with the plant life which furnishes its food and with its fellows in the obvious mechanical effects of crowding, the struggle for food and the demands of reproduction. If we concentrate upon the association of the individual with others of its kind we see that its environment is very different from the uncrowded pond where its ancestors lived. Its relationship with the others is variable, hence there is no visible change, but we can not fail to realize that its pushing, crowding, dodging progress is in itself a difference resulting from this association, which may be accompanied by others beyond our powers of observation.

The first cleavage of the ovum establishes such a relationship of like with like, save only that this relationship, far from being fleeting and variable, persists and gives rise to greater complexity. According to the logic of evolution there was a time when all organisms were single celled, like our jar of Colpoda, and there must have come a time when, for some unknown and unknowable reason, the simple reproductive division of one of these primordial organisms was not followed by the separation of the resulting cells. Instead the permanent association of like with like resulted, as in the primary cleavage of the ovum, and for the duration of existence the life of each was complicated by the presence of the other. Step by step we may trace this process into the formation of the complex body, where the organism as a whole has a relationship with its outer environment but in addition itself constitutes an environment where every organ, every tissue, every cell, has a part. There is, in other words, an internal environment, in addition to the complex environment of the outer world.

The relationship of the organism or any of its parts to this environment is complex in detail, yet simple in principle. The organism possesses certain physiological properties, but can do nothing except cease to live with-

out appropriate association with the manifold environment. At first thought the normal does not seem to be an active stimulus, but can it be otherwise? In the initial steps of ontogeny, which seem as remote from environmental effects as any living process, this possibility may be examined. Loeb's researches with the eggs of invertebrates are excellent detailed illustrations, but for the purposes of this paper unnecessarily so. Consider even the response of the hen's egg to temperature. Ordinary temperatures retard its development, while extremes kill it, but at the normal temperature of the species it develops; the most active response is the last. That this normal stimulus is a constant thing is graphically illustrated by Walter's "triangle of life,"[11] in which every organism is represented as a heritage and an environment to which it responds. In this connection we must not overlook the fact that every part of the organism is also an entity responding at least to the internal environment. The modern idea of the unity of the organism[12] is valuable but probably not the whole story.

As a second principle in our inquiry we may therefore state in summary that environment is an essential accompaniment of life and consists of anything not an integral part of the organism or organic structure under consideration, thus involving an external environment divisible into inorganic and organic complexes, and the internal environment.

IV

It is the purpose of this paper to inquire how these fundamentals of life cooperate in the determination of individual qualities, and to interpret phylogenetic modification on a basis of similar response in the chromosomes. Since the effect of such interpretation is largely to validate belief in the transmission of so-called acquired characters, it is first necessary to arrive at a definite understanding of the characters which have been considered

[11] Walter, "Genetics," Revised Ed., p. 4, 1923.

[12] Ritter, "Unity of the Organism," I, 1919.

in this connection. Walter[13] has classified these characters briefly as follows:

(a) Mutilations
(b) Environmental effects
(c) The effects of use and disuse
(d) The transmission of disease
(e) Immunity
(f) Prenatal influences

Without attempting to consider Walter's treatment of these categories in detail, certain pertinent facts may be taken up. To the first category, mutilations, we may add such mechanical modifications as the curling of hair. These are distinctly things impressed upon the organism by its environment, with no demand for organic response. They need not be considered further, for existing data are sufficient to convince us that they will never be inherited. The last category may also be discarded, for, as Walter notes, unless the health of the mother be seriously affected, there is no reason to suppose that anything in her environment will find direct expression in her unborn offspring.

In all other categories we note a very different condition. Environmental effects, such as sunburn, shaping of the head by mechanical means, as practiced by various aborigines, Kammerer's modifications of salamanders and a great variety of other well-known characters, are definite individual acquisitions, associated with definite conditions of environment, but they involve equally definite response of the organism, bringing to expression its inherent powers of development. That such modifications are so conditioned is well illustrated by the varying degrees of response to sunshine in the human race, ranging from repeated burning without adequate deposition of protective pigment to the mulatto shades of life guards at our beaches, gradually accumulated through long-continued exposure, not to mention freckles and the absolute inability of the albino to deposit pigment under this or any other stimulus.

13 Walter, *op. cit.*, p. 74, 1923.

Use and disuse is rather more complex, but here again the behavior of the organism or part is intricate and involves some condition of its environment as here defined, as well as an inherent power to respond. In this case it will be profitable to consider a few specific instances. Callosities arising in the individual are due to the repeated contact of an area of skin with external objects. They involve, obviously, the mechanical stimulus and the ability of the organism to develop thicker or more horny epidermis in response. Inherent callosities, or the more moderate case of thickened skin on the soles of the feet of *Necturus* have entered into discussions on the inheritance of acquired characters in many cases. Walter regards the condition in *Necturus* as in no way an acquisition,[14] since these animals do not use their feet to support their weight, and in the normal Weismannian manner are not supposed to have had ancestors which did so. Detlefsen[15] wisely questions the validity of this assumption. Indeed, we see elsewhere in the literature on evolution that the development of the pentadactyl appendage is one of the steps in the evolution of the terrestrial vertebrates. Granting the correctness of this view, it follows that *Necturus* had ancestors with sufficiently terrestrial habits to necessitate the use of the feet for locomotion on a solid substratum. In any event, such a case illustrates the weakness of arguments for evolutionary processes when applied to specific cases. We can probably never accumulate such complete data as would be necessary to the accurate judgment of these cases, but in all such the possibility, even the probability, must be admitted that there has been in the past, if there is not now, an environmental condition correlated with the existence of any structure. Training is also included in this category, with the indication that "the strong arm, the skilled hand, and the trained ear are not inherited." In considering these effects of use, we should consider also the effects of

[14] *Id., op. cit.*, p. 79.

[15] Detlefsen, *Physiological Review*, V, p. 248, 1925.

amphimixis, which may play a great part in the failure of a virtuoso to produce an equally able son, and the proper interpretation of the necessity for repeated training, generation after generation. The hereditary qualities of an individual enable him to do something. He may avail himself of the accumulated knowledge of our civilization to express the ability to the utmost. That utmost may be superior in one individual and mediocre in another. The two may have had the same environment and made an equally good response, but with different inherited powers. What they succeed in doing is an expression of response, whose heritability can not seriously be expected. The effect on the inherited power of similar response to similar conditions is another question entirely.

The transmission of disease, again as might be expected, is looked upon as impossible. Diseases as treated are also a response, in this case to the organic environment, and the same remarks apply as concern the inheritance of training. This is also true of the remaining categories of immunity and the effect of drugs. There is no proof that such characters are inherited, but we find significant cases of immunity to blood parasites in the association of African ungulates with trypanosomes which are often fatal to domestic cattle. At some time in the past the immunity has become inherent; the species has incorporated in its inheritance some power which makes possible tolerance of the parasites.

Although these several categories have been treated separately they fall readily into two, as brought out in the preceding paragraphs, *viz.,* characters solely due to the environment, literally forced upon the organism, and those which involve organic response to a definite condition of environment. The first are obviously of no interest to us; the second we must analyze further.

We speak of use and disuse, as of the muscles, the vocal organs, and other parts in terms of everyday language, but when analyzed the daily dozen becomes merely the

exercise of the inherent functions of various parts of the body. Such exercises involve components of the external environment, but they are mostly an excellent example of complex response to purely internal stimuli. Avoiding psychological complications, we may say that such benefits as accrue are due to the repeated contraction of as many muscles as possible, and to concomitant activation of other organs. In a like manner the mechanic uses his hands repeatedly to do certain tasks and is finally able to manipulate his tools and materials with a high degree of skill. He has, after all, merely exercised repeatedly the functional powers of muscles, nervous system and sense organs. If the body is attacked by the germs of a disease, and after recovery is immune for life, is it any more than a result of the exercise of a certain inherent power to function? Yet it would not have exercised this power without the activating stimulus from the environment. In short, use is merely the exercise of functions, more or less complex, and disuse the failure to exercise them, so that any significant acquired characters may be interpreted as the results of use or disuse of some inherent function.

Use and disuse in somatic tissues have an effect on the functional capacity of the structures involved, as indicated by increased power of contraction in muscles, increase in visual power, in tolerance for poisons and in thickening of the skin, as well as the decrease of such powers.[16] In many cases of ordinary experience we note that these processes are cumulative. It takes many months, even years, to realize the maximum expression of any individual power, and even then it can be attained only through repeated exercise. Likewise the neglect of a part must be complete or nearly so if an appreciable atrophy is to be brought about. Moderate use results in proportionate development, but equally familiar cases indicate the deleterious effects of extreme exercise of function, although the limit appears to be very indefinite,

[16] Morgan, "Evolution and Adaptation," p. 12, 1903.

provided only that it be approached by gradual steps. This is perhaps nowhere more strikingly illustrated than in the reaction of the human body to arsenic, as detailed by Morgan,[17] who states that the dosage may be increased gradually to an amount sufficient to kill ten men, and decreased in a like manner to a point where it may be discontinued entirely, although sudden discontinuance or administration of the maximum amount would be fatal.

It seems not extreme, in view of these considerations, to regard all functional activity as use, and all rest as disuse, both involving the response of some part or parts to definite conditions of the complex environment. Nor does it seem illogical to apply generally the principle established in so many cases that the exercise of a function results in increased ability to exercise it, and *vice versa*. Returning to the first interpretation undertaken in this paper, there is apparently no valid reason for excluding the chromosomes from consideration, as specialized organic matter, under the same principles, but inasmuch as the exercise of their functions in full occurs but once in a generation, a duplication of the conditions of somatic development in phylogeny in respect to repetition would involve the long periods of geological time, with long continuation of the same environmental condition. The results could not but approximate our geological record of evolution. Effects of environmental stimulus are differential. One change may affect the use of a pair of appendages. The determining power of the chromosomes is then realized in the particular way and degree which constitute the response of the organism. If the conditions persist in a succession of generations, we may expect a cumulative increase of this functional power, as actually occurs in parts which can be subjected to observation. As a part of the coordinated body, although more completely diffused than any other specialized part, there is reason to believe that the chromosomes will respond to such stimuli wherever they may be lo-

[17] *Id., op. cit.*

cated, in germ cells as well as in somatic cells, and with a change once initiated, it is impossible to say what further changes might be brought about by adjustments of the internal environment. Such a process would necessarily mean a gradual modification of existing structures, and here again the theory fits the observed facts.

Use and disuse in the chromosomes is therefore not an illogical explanation of the ultimate incorporation in the heritage of those characters which first appear as individual adjustments to the environment. It is wholly in harmony with the obvious correlation and mutual importance of environment and heritage in the development of organisms. While it does not explain ultimate sources, it does adequately account for transitions from structure to structure through gradual modification in response to continued environmental conditions, and for a development of internal environmental conditions which might bring about even non-adaptive modifications. Thus it refers all change to a single ultimate source in primordial living matter, and this is perhaps all that we can hope for in the present.

CHANGES OF ENVIRONMENT AS CAUSE OF THE ORIGIN OF VARIETIES OR SUBSPECIES

DR. N. A. BORODIN

It seems to me that a study of so-called relict forms may elucidate to some extent the question whether or not a variety (subspecies) or species may arise due to the changed environment. Relict forms can not be reasonably explained without considering the geological changes which have taken place in the locality where they were found and without studying their nearest relatives in areas earlier connected with the one in which they are found.

About thirty years ago I made a biological survey of one of the brackish lakes of southern Russia, namely Lake Tscharchal, which is situated about forty miles south-southeast of the town Uralsk on the Ural River—a boundary between Asiatic and European Russia. The lake has a circumference of thirty-two miles. There are two small creeks (Ankatas) feeding it. An old semi-dried channel (Solianka), about sixty miles long, connects it with the Ural River, which runs into the Caspian Sea. This connection was complete, however, only in the remote past; at the present time the lake is isolated—its distance from the Caspian Sea about 350 miles. In the post-glacial period, the waters of a huge sea, Mare Aralo-Caspio-Ponticum, covered this entire area and the surrounding country, including the Aral, Caspian and Black Seas and the steppes between them (see the map).

In the course of geologic time, namely, about the second glacial epoch of the Pleistocene period, the Black Sea was separated from the Caspian. Later, the Aral Sea separated from the Caspian. At the same time a waste area, previously covered by water, became land as the Caspian Sea receded more than three hundred miles from north-east to south-west. During this great recession many

small lakes were formed in depressions of the former sea bottom. Most of them became salt lakes, but those which received a water supply from rain, snow and affluents became brackish water lakes.

It is in the latter category that Tscharchal Lake, the fauna of which we are considering, belongs. It is comparatively deep, in some places from fifteen to eighteen and a half feet in depth. The salinity of its water is 0.039, while that of the Caspian Sea is from 0.075 to 0.15.

My interest in zoological exploration of this relict lake was concentrated on fishes in which it is very rich, and I found there the following species also occurring in the Ural River: *Leuciscus rutilus* L. var. *vobla,* Yakovlev auth.; *Abramis brama* L.; *Pelecus cultratus,* and some others. However, in addition to these, I found in abundance a species of small herring similar to that occurring in the Black Sea, but which does not occur either in the Ural River or in the Caspian. This was described as a variety of the Caspian Sea species, *Clupea cultriventris* Nordman,[1] var. *Tscharchalensis* Borodin.[2]

[1] Nordman. Faune Pontique. 1840, p. 522.

[2] Borodin, N. "Note on the Herrings of the Black and Caspian Seas." *Ann. Rep. Mus. Zool. Acad. St. Petersburg,* 1896, 1. pp. 81–94 (Russian).

In view of the separation of the Black Sea in a geological epoch some three hundred and fifty thousand years ago, and the withdrawal of the Caspian about two hundred thousand years ago, we have some time measure of this subspecies which must have been formed by isolation and the changed conditions of life incident to being shut off in an isolated lake. As there is no other means of explaining its presence, we have here a very good proof of the development of a new variety or subspecies given a sufficiently long period of time. This form may be easily distinguished from its nearest ally living in the Black Sea—*Clupea cultriventris*—and still more easily from the species living in the Caspian Sea—*Clupea delicatula* Nord. In fact, Dr. L. Berg considers it of full specific rank, *Clupea tscharchalensis* Borodin.[3] Its most

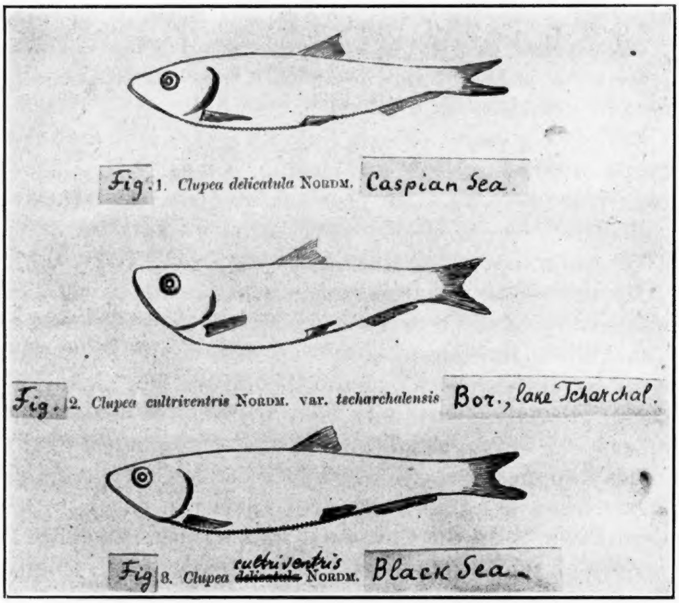

Fig. 1. *Clupea delicatula* NORDM. Caspian Sea.

Fig. 2. *Clupea cultriventris* NORDM. var. *tscharchalensis* Bor., lake Tcharchal.

Fig. 3. *Clupea* ~~*delicatula*~~ cultriventris NORDM. Black Sea.

[3] I retain the genus *Clupea* for simplicity and clearness. According to Dr. L. Berg's more recent classification ("Fresh-water Fishes of Russia." Moscow, 1916, p. 32), it should go in the genus *Harengula*.

striking character is a very deep body and peculiar shape (see Fig. 2). It may be worth while here to review the fish's characters as compared with Caspian and Black Sea forms.

C. tscharchalensis	*C. cultriventris*	*C. delicatula*
Tscharchal Lake	Black Sea	Caspian Sea
Depth $3\frac{3}{4}$ in the length	Depth $4\frac{1}{4}$ in the length	Depth $4\frac{3}{4}$ in the length
Profile of the back straight	Profile of the back slightly convex	Profile of the back arched
Belly knife-shaped, sharply convex	Belly moderately convex	Belly slightly convex
Head and mouth looking upwards	Head and mouth on middle line	Head and mouth on middle line
Gill rakers 43	Gill rakers 45–55	Gill rakers 44–56

Being related to both Caspian and Black Sea species, the small Tscharchal herring diverged and became specifically distinct as a new form in this long isolated lake, which also presented quite a different environment and climate (as it is covered with thick ice for a long period in winter), had a lower salinity, different food supply, etc. All these factors of importance to the living fish working over a protracted period in the end differentiated what I consider a new subspecies and Berg recognizes as a new species.

In spite of strong opposition, an authoritative group of contemporary naturalists, among whom may be mentioned H. F. Osborn, advocates as a fundamental factor in evolution what Osborn calls "*speciation,*" a peculiar phenomenon [which] can be observed and traced to the oldest geological period of animal life, namely, the slow modification in the structure of the organisms under the influence of changed life conditions."

Speciation (as distinguished from mutation) consists of changes which result in the formation of new varieties and species over a long time period. He says that for the formation of species not less than twenty thousand years (since the glacial period) is needed. Isolation of basins helps such formation. This phenomenon (speciation) is clearly stated for all the great families of animals[4] and he further quotes a series of statements made

[4] H. F. Osborn. "Address at the Meeting of the British Association for the Advancement of Science." *Science,* October 8, 1926.

by various specialists each for his particular field. The case of the subspecies of the small herring from isolated Lake Tscharchal, it seems to me, may be looked upon as additional evidence supporting the above opinion on the origin of species under changed environments.

A closer comparative study of the ichthyological faunas of the three seas—the Aral, the Caspian and the Black—which were previously joined and are now separated, might provide further similar, and, perhaps, even more convincing, evidence. Let us consider the fishes of the family Clupeidae, the representatives of which have during the last twenty years been studied more closely than any other family of fishes inhabiting these seas.

The first important point is that the herring-like fishes of these three adjacent bodies of water which were once in communication and in a single basin, differ very notably. The Caspian is inhabited by four species of the genus *Clupea* Linn. (*Caspialosa* Berg) and two species of *Harengula* Val. (formerly *Clupea* Linn. and *Clupeonella* Kessler-Berg). In the Black Sea there are two different species of *Clupea* (*Caspialosa*) and one different species of *Harengula.* In the Aral Sea not a single representative of this family is to be found. A closer analysis of the Caspian species of *Clupea* (*Caspialosa*) shows that they fall into two categories—marine and fresh-water—and that the marine species resemble somewhat the common herring of the ocean. To the first group belong *Clupea saposhnikowi* Grimm; to the second, *Clupea caspia* Eichwald and *Clupea kessleri* Grimm. *Harengula grimmi* (=*Clupea engrauliformis* Borodin) is found only in the Caspian Sea. *Harengula delicatula* Nordman is found in the Caspian as well as in the Black Sea, though in the latter it has changed slightly in exterior shape and has been described by Nordman as a variety named *Clupea cultriventris.*

Other species of herring of the Black Sea, *C. pontica* Eich. and *C. tanaica* Grimm, differ notably from the Caspian species and are both anadromous fresh-water fishes.

Taking into consideration all that is said above, one can not help reaching the conclusion that all the species of the Caspian and Black Seas have arisen recently, in the geological meaning of the word, since the time at which these seas were separated one from the other. Thus, the formation of a species during several hundreds of thousands of years (since the second interglacial stage of the Pleistocene period, when, according to Professor N. Androusoff, a Russian geological authority, the separation of the Black and Caspian Seas took place)[5]—must be admitted to be almost an established fact.

Some mention should be made of other points concerning the herring-like fishes of the Caspian and Black Seas. In both the seas there are species adapted almost exclusively to fresh water—*C. caspia* Eich. in the Caspian Sea and *C. tanaica* Grimm in the Sea of Azov, which is that part of the Black Sea with lowest salinity.

In 1896, speaking of the herrings of both seas,[6] I expressed the opinion that *Clupea saposhnikowi* Gr. in the Caspian Sea, the form closest to the marine herring, is a relict marine form changed under new conditions; that it is less adapted to the local conditions than are the semi-fresh-water forms, *C. caspia* and *C. kessleri,* which are more numerous though more restricted in distribution (they are found only in the northern portion of the Caspian with water of low salinity). I furthermore predicted that more thorough study of the herrings in the Sea of Azov would bring to light a fresh-water subspecies or more intermediate forms. In line with this prediction, in 1901 Dr. Grimm found there and described a new species, *Clupea tanaica,* which corresponds to the Caspian *Clupea caspia* Eich.[7]

[5] "Sketch of the Historical Development of the Caspian Sea and its Inhabitants." By N. Androusoff. Bulletin of the Imperial Russian Geographical Society, 1904–05, vol. XXIX.

[6] N. Borodin. "Note sur les clupéidées des mers Caspienne et Noire." Annuaire du Musée Zoologique. St. Petersburg, 1896, Tome 1.

[7] O. Grimm. "Die Herringe der Azov'schen Meeres." Aus Nikolsk Fischzucht Anstalt. St. Petersburg, 1901, p. 4.

DUPLICITY IN BIRDS

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THE literature on double monsters is voluminous and includes mention of cases in all the classes of vertebrates. Frequently the reports are confined to brief statements regarding the external characteristics of the subjects, while the mass of theory developed is by no means limited by the facts actually at hand.

During several years past, it has been the fortune of the writer to have the opportunity to examine several specimens of double chicks and one double duckling. In some of the specimens preservation was so excellent that much of the internal anatomy could be studied, and it is hoped that the facts here recorded may be of some interest to anatomists.

SPECIMENS STUDIED

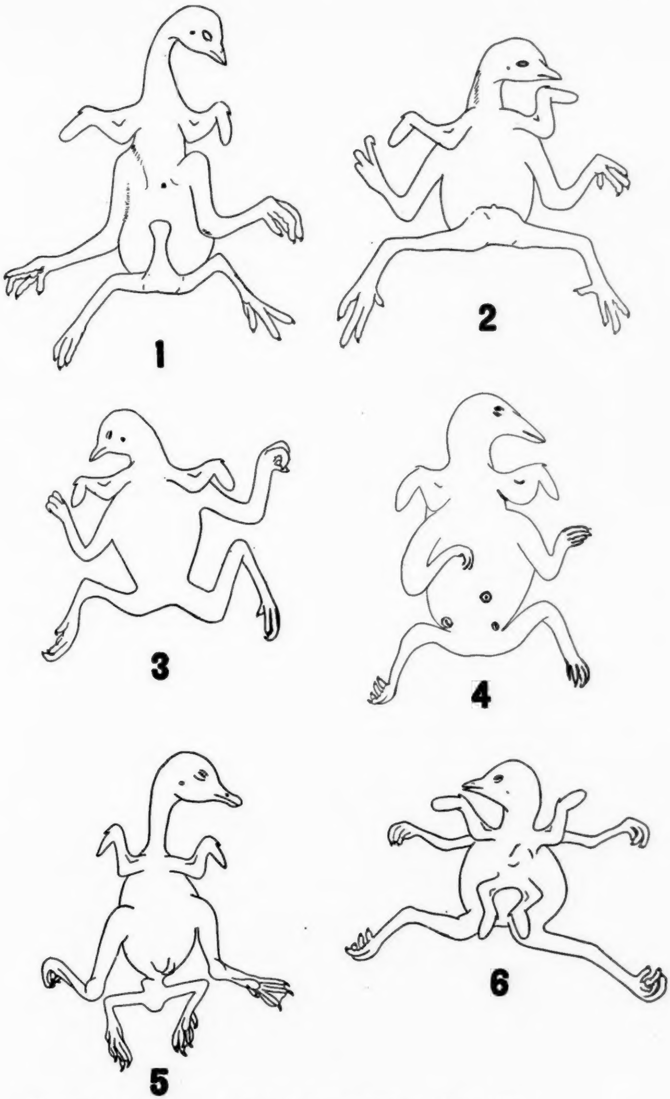
The specimens studied may be grouped into two classes:

(1) Two wings, four legs. New Jersey Collection. Figures 1, 2, 3, 5. West Virginia Collection. Figure 4.

(2) Four wings, four legs. New Jersey Collection and duplicate from West Virginia Collection. Figure 6.

In the specimens with four legs and two wings, there was considerable variation in the attachment of the legs. In the cases represented by Figures 2, 3 and 4, the hinder pair of legs arose from the posterior part of the pelvic girdle, while the anterior pair arose from positions immediately behind the pectoral appendages, connecting with thoracic vertebrae.

On the other hand, in the case of the chick shown in Fig. 1, and also in the duckling shown in Fig. 5, it is evident that the anterior and posterior pairs of legs have arisen in front of and behind the normal origin but at no considerable distance from each other.



Figures 1, 2, 3, 4. Chicks with two wings and four legs.
Figure 5. Duckling with two wings and four legs.
Figure 6. Chick with four wings and four legs.

The skiagraphs of specimen 1, seen in Figs. 7 and 8, also serve to emphasize the closeness of origin of the two pair of legs.

All the specimens had double cloacae, and these varied in location from the condition represented in Fig. 4, to that represented in Fig. 9, a photograph of specimen 6, which last indicates clearly how the four-winged, four-legged monster has approximated the appearance of two animals in one. Fig. 9 emphasizes the lateral disposition of the two cloacae.

Internal Anatomy

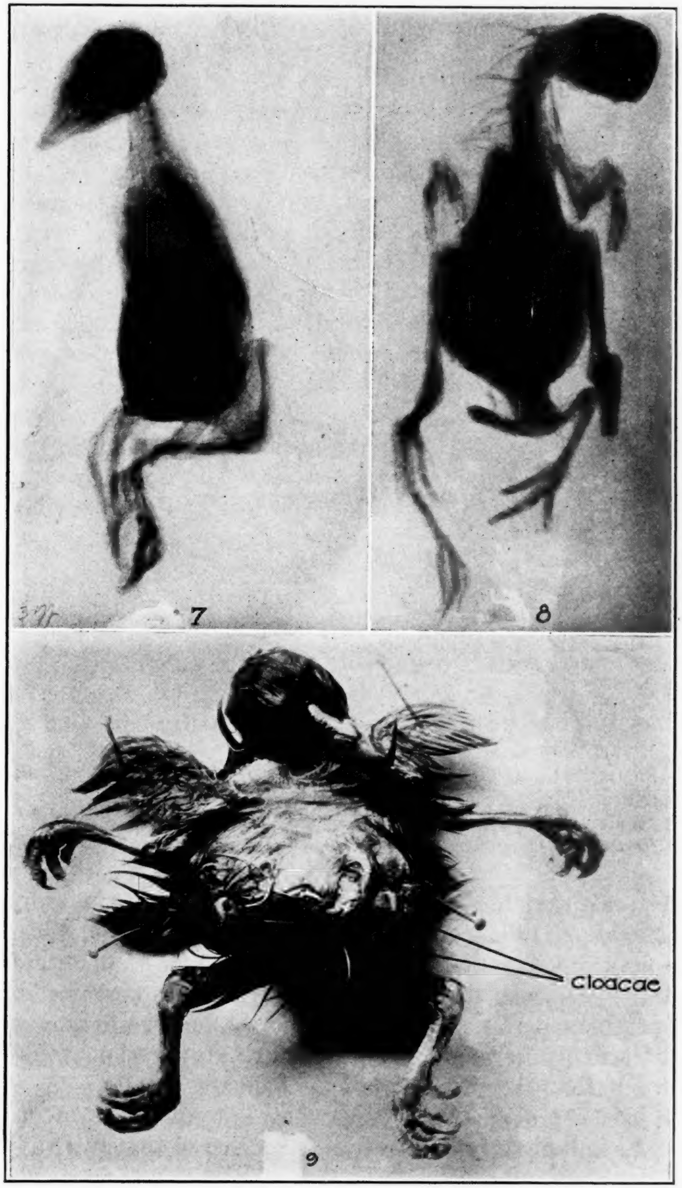
Careful study of the specimens shows that the duplicity was a posterior one in all cases, as there was no evidence of doubleness in heart or respiratory apparatus.

However, in spite of the fact that the proventriculus and gizzard remained single in all cases, there was considerable variation in the remainder of the digestive tubes.

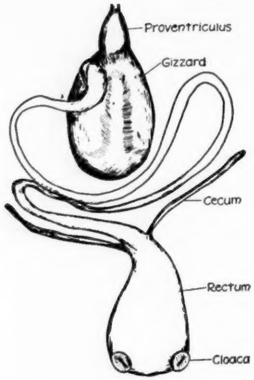
It is worth passing mention that in otherwise normal chicks there may be a double cloaca. Fig. 10, illustrating an enormous rectum and two cloacae, is of a chick that was otherwise perfectly normal.

In Fig. 11, the digestive tubes of a four-legged chick with normal wings (see Fig. 4 also) are represented. The cecae on the left side of the animal, two in number, correspond to the normal ones, and it is of interest to find that, as shown so well in the drawing, Fig. 4, the left cloacal opening approximates its normal position. On the other hand, we must note that the cloacal opening seen far to the right in Fig. 4, has attached to it the large rectum, pulled to one side, while only a single cecum has developed. Evidently the duplicity was completed for the digestive tube on one side only.

In the case of the four-winged, four-legged chicks represented by Figs. 6 and 9, the digestive tubes were double behind the gizzard. The drawing (Fig. 12) shows that the tubes continued after their separation and were in no



Figures 7 and 8. Skiagraphs of chick shown in Figure 1.
Figure 9. Photograph of chick shown in Figure 6, showing cloacae.



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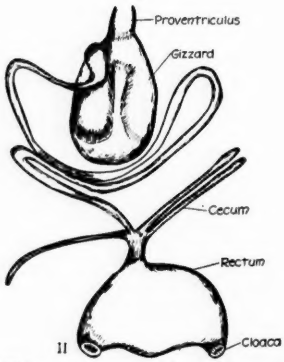

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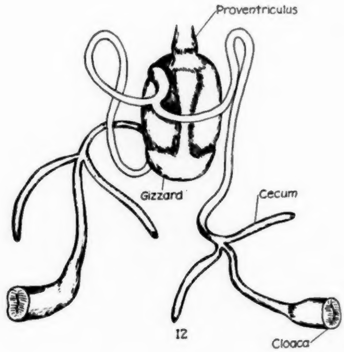

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Figure 10. Double cloacae in an otherwise normal chick. (Wells specimen.)

Figure 11. Digestive tract of specimen 4.

Figure 12. Digestive tract of specimen shown in Figures 6 and 9.

wise abnormal, although they might be said to mirror-image each other. The small intestines, the paired cecae and the two rectal enlargements were in no wise abnormal and connected with their respective cloacal apertures in such manner that if one did not find the legs arranged abnormally he might conclude that an operation would divide the posterior parts of the monster equally.

In most of the specimens the reproductive systems were so immature and so poorly preserved that it is dif-

ficult to state the relationships. In the case of the kidneys, however, it became evident that there was a gradation in the conditions existent. In the case of the specimen with two cloacae and normal legs, the kidneys were normal in position. In the case of those specimens that had two wings and four legs, it was possible to determine in one specimen that there were but two kidneys. Three lobes were distinguishable on the right side of the right pair of legs, and the three lobes of the left kidney were located at the other side of the body, at the left of the legs of that side. In the case of specimens with four wings and four legs, the kidneys were also doubled, and the posterior duplicity undoubtedly extended to the reproductive system also.

The spinal cord was double from the cervical region posteriorly in all the specimens. Apparently those organs supplied by the cerebral nerves were single, while the remainder were double.

General Considerations

The specimens were all posterior duplicities. In fact, it appears that anterior duplicity is relatively infrequent in those chicks that come to the hatching period. Bryce (1899) found that of ninety-five cases described but four were of anterior duplicities.

There was a quite evident gradation in the specimens, with the internal structure corresponding. In the subjects with two wings and four legs there were in two cases but three cecae instead of four.

In the specimen with two wings and four legs in which it was possible to distinguish the kidneys, the notable separation indicated that there had been a fission posteriorly. This is in accord with the evidence from Gerlach's observations (1882) of a chick embryo of sixteen hours which he actually saw in the process of bifurcation.

Tannreuther (1919) has studied a number of cases of very early duplicity in the chick, including a specimen in which there is a single head back to the mesoblastic

somites. Behind that the two bodies diverge at an angle of 120°. That the double embryo began as two independent primitive streaks, with later fusion of the anterior ends, seems most unlikely. Newman (1923) has pointed out that such fusion with perfect symmetry to form one head would be a most difficult procedure.

SUMMARY

(1) Of seven specimens of posterior duplicity in the bird, two were cases of four wings and four legs, the remainder had duplicity of the legs only.

(2) Considerable variation occurred in the attachment of the legs, and in all cases the spinal columns were double posterior to the cervical region.

(3) Internally, the digestive tracts were double behind the gizzard, with either three or four cecae present.

(4) The kidneys were duplicated in specimens with four wings and four legs, but in one of the cases of two wings and four legs the anlage of the kidneys had divided and there were but two kidneys, widely separated.

(5) All the cases evidently resulted from posterior fission, as it would be most difficult to conceive of perfect fusion of the heads from independent primitive streaks.

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SHORTER ARTICLES AND DISCUSSION

GENETICS AND THE PROBLEMS OF DEVELOPMENT[1]

In a recent paper Morgan (1926)[2] has pointed out the significance of certain findings in heredity for the student of developmental phenomena. He urges the necessity for adequate control of the variable, hereditary constitution, in physiological experimentation and with a few well-chosen examples illustrates what the Mendelian understands by genetic determination. The several attempts which have been made to interpret some facts of growth and differentiation in terms of gene action are reviewed in characteristically incisive fashion. It is not our purpose to comment upon the generally constructive criticisms offered on these points or upon the author's interesting suggestions regarding the possible relations between genes and enzymes. We should like, however, to examine further certain implications of the gene theory for the processes of development and to attempt to set out in more clear-cut form an important opportunity which genetics offers the physiologist; as a rather indefinite undercurrent in Morgan's discussion the idea seems to have escaped the emphasis we believe it deserves.

The Mendelian theory postulates discrete, self-perpetuating, stable bodies—the genes—resident in the chromosomes, as the hereditary materials. This means, of course, that the genes are the primary internal agents controlling development. It has never been shown that the cytoplasm does not, in some degree, maintain an integrity of its own; but if it does it is of a much less definite sort than that of the nuclear units. Given a certain set of external conditions, then, the course of development proceeds according to the character of the gene complex present.

It is patent to every one that ontogenetic processes may be enormously influenced by environmental circumstances also. We have the two variables, therefore, heredity and environment, determining the character of development. Now what the geneticist is accomplishing for the physiologist is an itemizing

[1] Papers from the Department of Genetics, Agricultural Experiment Station, University of Wisconsin, No. 67. Published with the approval of the director of the station.

[2] Amer. Nat., 60: 489–515.

and cataloging of the elements in the one variable, heredity. He is resolving the internal complex into its constituent units. The student of development may object that the catalog which the geneticist furnishes him is of little real aid because what he most wants to know about the unit is not there, namely, its dynamic properties. It is as though an employer in search of mechanics were handed a general directory, giving name, street and number but with the occupation column vacant or blurred in the press.

It is true that some of the things about which the geneticist has learned a great deal, such as arrangement of the genes in the chromosomes, have no apparent significance, at present at least, for the problems of development. We think, however, that the central feature of the Mendelian theory—the concept of the gene—has not been accorded the place in the physiologist's thinking that its importance warrants.

Up to the present time the methods used in studies on developmental physiology have embraced almost exclusively the means which controlled changes in the environment afford. The investigator has devised ingenious ways of varying the external factors independently of each other and his progress is in large part proportionate to the degree to which he has been able to resolve these factors and to control them. He has built up a highly effective technic by which the action of the one set of variables comprising the environment may be studied.

Now what we should like to emphasize beyond the point to which Morgan carries the thought is that the other variable, heredity, in the workable form in which the geneticist has put it, furnishes the physiologist with a wholly new kit of tools which promise to be as effective in the analysis of developmental processes as the environmental agents he has been accustomed to use. To hold the genetic constitution constant and run the scale of certain external factors is the standard method; but with the primary internal mechanism resolved into definite units which may be combined in various groups, the way is open for an attack from the opposite direction. The hereditary complex need not longer serve merely as the passive object in physiological experimentation but may itself be varied in a precise fashion and within limits coextensive in their effects with the extremes of environment. We are now in a favorable position to get at the dynamic properties of the hereditary mechanism by means of an analysis

of the action of its separate elements. This, it seems to us, is the signal contribution which genetics makes to our outlook upon the problems of developmental physiology.

What genetics offers is the opportunity to change the machine itself within certain limits. We can not pick it apart, of course, and study the rôles of its multitude of constituent parts individually, but we can vary certain functions *in situ* by substituting one allelomorph for another. The mutant races of a given species may be looked upon as physiological systems differing in one or more discrete germinal units. By comparative physicochemical studies we may be able to discover the dynamic properties of these hereditary elements. It goes without saying that in gaining an understanding of the specific character of developmental changes this would be highly useful information. No one who has tried this method, to be sure, entertains any illusions as to the difficulties involved, but nevertheless it appears to be a very hopeful means of extending our knowledge of the mechanics of development. At least it is worthy of far more extensive trial than has yet been given it.

The question may appropriately be asked as to where in the life cycle this new tool is to be brought to bear on developmental problems. The geneticist, so far as he has concerned himself with the action on the organism of the genes postulated, has worked at one end of the ontogenetic scale, so to speak, and the embryologist at the other. The former has identified his factors, generally speaking, by their effects in the adult and has little to offer regarding genetic differences in the early stages of development. Perhaps a profitable working relationship with the student of early developmental physiology can not be established at the present juncture, for it would seem that the differential genetic effects coming latest in development offer the best opportunity for physiological study. It has seemed to the writer that there may well be a rough correspondence at least between the extent of the effects of a gene on an organism and the stage in development at which the gene comes into play; the earlier in ontogeny that a primary differential action of a given sort occurs the greater the number of secondary effects it may occasion. One might venture the suggestion that many of the frequently arising lethal genes may primarily condition processes occurring relatively early in development; the first change called forth by the gene may not be disruptive in itself, but it must run the

gamut of a long series of succeeding events any one of which may be unable to accommodate itself to the altered circumstances. The albino seedling in maize, for example, grows readily enough until the necessity for photosynthetic activity arises. However this may be, we may consider it a sound working principle that the genes whose primary physiological actions prove most accessible to analysis will be those which do not come into play under conditions in which they may impinge upon a large number of processes and thus obscure their main properties by secondary effects. In general, we should expect the fewest cross-currents in connection with specific reactions occurring late in development.

What the student of comparative genetic physiology should seek in his attempts to reveal the dynamic properties of genes, therefore, are differential effects coming at the end rather than at the beginning of the series of developmental changes. What he wants particularly are heritable variations affecting processes at the termini of open systems. Possibly these may provide a fair sample of the different classes of gene action.

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A STUDY OF GYNANDROMORPHIC KATYDIDS

Cytological contributions describing the chromosomal condition present in gynandromorphs have been lacking due to the difficulty involved in finding a species in which gynandromorphic individuals may be detected when the cells are rapidly dividing, and at the same time be suitable for chromosomal study.

Accidentally I found two gynandromorphic katydids belonging to the genus Amblycorypha. This material was exceedingly favorable for study in that the abnormal individuals were distinguished during the nymphal period by color differences. They belonged to the simple XX-XO type. The chromosomes were large and the X-chromosomes at least twice the size of the largest autosome.

The material was collected at the Indiana University Biological Station, Winona Lake, Indiana. The cytological study was made last semester as a graduate student at Columbia University.

The first individual (third? instar) possessed on the right side

a normal half ovipositor with the upper, lower and inner valves well developed. On the left side there was a single large scale-like valve which was somewhat shorter than the normal valves. It was applied so closely to the normal half ovipositor that the specimen would have been mistaken for a female if the color had not been that of the male. Internally a compound gonad was present on each side. Each gonad was composed of a compact ovary and testis, both types of tissue being about evenly divided in volume. The ova were located in normal well-developed tubules and the cysts of the testis were normal. A pair of apparently normal oviducts were present, each acting as a common duct receiving the tubules from both male and female tissues. Spermatogenesis was like that in the normal male. The spermatogonial count was one X-chromosome and thirty-two autosomes. The female tissue contained two metaphase plates that were favorable for a chromosomal count with difficulty. Each of these contained two X-chromosomes. The autosome number was uncertain. A very careful study of these plates, however, showed the first plate to contain no more than thirty-four nor less than thirty-two autosomes, and the second plate no more than thirty-five nor less than thirty-two.

The second individual (fourth? instar) was externally a normal female with the male color. Internally a normal ovary was present on one side while the other side contained a double gonad with the testicular tissue predominant. A common duct led from the latter side. The ducts from the two sides were apparently normal oviducts. The other structures of the internal genitalia were like those of the normal female. The spermatogenesis was like that of the normal male. There were no countable plates in the female tissue, but two X-chromosomes were present.

A third specimen, which probably belonged to a different species, was not observed to be abnormal in the field. It seemed to be a normal male with the exception of one testis containing a single ovarian tubule of very small size. No countable plates were present in the female tissue. It was interesting to note, however, that the oöcytes in the growth period did not show the X-chromosome which was so characteristic in this material during the growth period of the spermatocytes.

Last summer collections were made in the same locality where the gynandromorphs were originally taken. Although several

times more individuals were examined than previously and the search made more extensive, it was unsuccessful.

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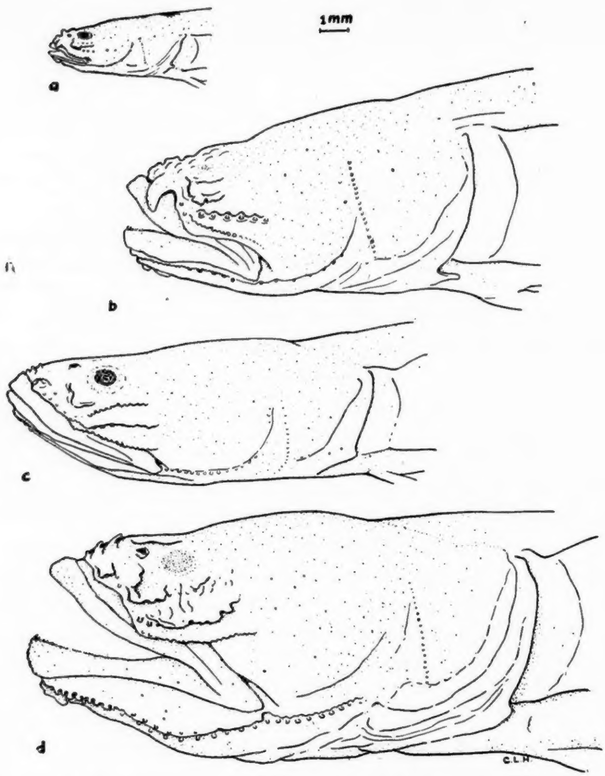
THE ORIGIN OF THE BLIND GOBY OF THE CALIFORNIA REEFS

THE occasion for again bringing the blind fishes out into the light has been the recent discovery, on the California reefs, of a fish, *Lethops connectens* Hubbs (1926). This fish seems to be related more closely than any previously known to the remarkable blind goby *Typhlogobius californiensis* Steindachner, of the same general habitat and region. No one before 1922 had ever seen *Lethops connectens:* it was quite new, both as to genus and species. The only adult specimen (Fig. *d*), which serves as the type of the species, was collected by poison in a reef pool of low tidal level at the village of Carmel, central California. Two other specimens (Fig. *c*), half-grown, were taken by the same means in a very rich, low rock pool at White Point, Los Angeles County, in southern California. The species therefore occurs in the two fairly distinct faunal areas of central and southern California. Its known range slightly overlaps that of *Typhlogobius californiensis,* which occurs from the reefs of Los Angeles County (including that of White Point, where *Lethops* was taken) southward to northern Lower California.

Concerning the habitat of *Lethops connectens* little definite information, regretfully, can be given, since the three specimens which now alone represent the species were all taken by poison. They were first seen in the pools about deep crevices in the rocks, from which they had doubtless been driven by the action of the poison. The taking of but three specimens in our very extensive collecting in the intertidal area of the California reefs indicates that the species occurs chiefly beyond the lowest tidal levels. The probable habitat of *Lethops connectens,* therefore, is the deep crevices in the rocky reefs, chiefly below the lowest tidal levels.

The habitat of the blind goby itself, fortunately, is much better known. It occurs on all the rocky reefs of the mainland shore of southern California (Hubbs, 1916, p. 165), whether the reef be exposed to the waves, or largely protected, as on the east face



Heads of *Typhlogobius californiensis* and of *Lethops connectens*.

All of the figures are drawn to the same scale, indicated at the top of the plate.

FIG. *a*. Young specimen of the blind goby, *Typhlogobius californiensis*, showing the degree of development of the eye.

FIG. *b*. Adult specimen of *Typhlogobius californiensis*. This specimen and the young both collected near Point Fermin, California.

FIG. *c*. Half-grown specimen, paratype of *Lethops connectens*.

FIG. *d*. Adult specimen of *Lethops connectens*: the holotype, from Carmel, California.

of Point Loma. In the locality last named the species has been taken in greatest abundance and is best known. It lives in the medium or higher tidal levels, therefore above the habitat of

Lethops, and in a most definite situation: namely, beneath stones, in the thus darkened burrows of a peculiar crustacean (Eigenmann, 1909, 1917, and other papers).

Two views concerning the relationships of *Typhlogobius* have been suggested. Jordan and Evermann (1898), in placing the genus in their subfamily Crystallogobiinae, indicate their interpretation of this genus as related to the equally remarkable *Crystallogobius*. But that goby differs widely in dentition and other characters. It is scarcely conceivable that the blind goby of the California reefs is in any close way related to this little, transparent, pelagic creature of northern Europe. They are perhaps as distantly connected as any two genera in the family. Eigenmann (1909, 1917 and other papers) has suggested, more plausibly, that certain burrowing or hole-inhabiting gobies of the enclosed bays and esteros of California (namely, *Gillichthys, Quietula, Ilypnus* and *Clevelandia*) are related to *Typhlogobius*. This view is quite probably correct, but none of those genera stand as near *Typhlogobius* as *Lethops* does.

The origin of the blind goby of the California reefs may be considered from two angles: (1) its origin as a reef fish; (2) its origin as a blind fish. An extensive study of the intertidal reef fish fauna of California has indicated strongly that nearly all the species have been derived from the reefs beyond tidal limits and not from the depositing shores of esteros and bays, nor from the surf along sandy beaches, certainly not from the pelagic area. The discovery of *Lethops connectens* brings the blind goby in these respects into alignment with the reef fishes as a whole, suggesting its origin from a fish of the infra-tidal areas of the reefs.

The discovery of *Lethops connectens* further indicates that the blind goby originated from a crevice-seeking form with the eyes already reduced and the tactile organs compensatingly more extensively developed than usually (see figures). *Lethops* bears the same relation to *Typhlogobius* that *Chologaster*, the "Dismal Swamp fish," bears to the other cave fishes (Amblyopsidae) of North America (Eigenmann, 1909, 1917 and other papers).

The eyes are quite as large, absolutely, in the half-grown as in the adult of *Lethops* and show to superficial view a clear distinction between pupil and iris, and a trace of a free orbital border. In the adult the eye exhibits superficially no apparent differen-

tiation of structure. The tactile sense organs of the head are excessively well developed and are larger in the adult than in the half-grown. The concomitant degeneration of the eye and increased differentiation of tactile organs thus marks the ontogenetic as well as the evolutionary line. The young of the blind goby, as shown in Fig. *a*, have developed eyes (as Eigenmann already has shown), but in the adult the vestige of the eye is hidden beneath the skin (Fig. *b*). The tactile organs, however, are in contrast very highly developed (see Ritter, 1893).

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